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RESOURCE SPACE PARTITIONING BY THE BRYOZOA OF A *FUCUS SERRATUS* L. COMMUNITY

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Abstract: The spatial distributions of five Bryozoa species encrusting *Fucus serratus* L. plants in Strangford Lough, Northern Ireland, have been examined in two cross-sectional samples yielding 80 plants and 1326 sampling units drawn from 13 environmentally diverse sites. The co-occurences of *Flustrellidra hispida* (Fabricius), *Alcyonidium hirsutum* (Fleming), *Electra pilosa* (L.), *Membranipora membranacea* (L.), and *Celleporella hyalina* (L.) on individual *Fucus serratus* plants were consistent with independent settlement onto each plant, but their joint distributions within the plants were markedly non-random. Measurements of behavioural interactions between species showed that competitive abilities declined through the sequence *Flustrellidra*, *Alcyonidium*, *Electra*, *Membranipora*, which parallels the sequence of competition (Levins' α) coefficients calculated from spatial distribution data. Competitive ability varied with position on the plant, *Flustrellidra* and *Alcyonidium* reversing their relative competitive superiority between basal and distal regions of the fronds. *Flustrellidra* and *Electra* were strongly associated under all conditions. *Alcyonidium* was also frequently present with this pair, though its numerical abundance was inversely related to that of *Flustrellidra*. *Celleporella* tended to co-occur with *Electra* whilst avoiding *Flustrellidra* and *Alcyonidium*. *Membranipora* numbers were inversely related to those of the other species. Analyses of competition coefficients showed that *Flustrellidra*, *Alcyonidium* and *Electra* each peaked in competitive ability against *Membranipora* at different points along the frond, such that the latter was effectively excluded by direct as well as by diffuse competition. *Membranipora* populations had a greater dependence on the segment area available for colonization than had any other bryozoan species.

INTRODUCTION

Marine intertidal macro-algae such as *Fucus serratus* L. provide suitable substrata for a rich and vibrant epifaunal community in which the Bryozoa are particularly well represented. Although competition between these sessile organisms in such a space-limited system is severe, competitive interactions within the bryozoan guild can be reduced by differential use of sites located in different environments, by differential response to the available plants, or by differential use of micro-environments within the one plant (O'Connor *et al.*, 1979). In this paper we examine four

factors: (i) the degree of isolation of the species achieved as to the plants colonized by each (thereby subsuming both site and plant characteristics), (ii) the isolation achieved within the plants and the mechanism involved in maintaining this, (iii) the level of competitive interaction present, and (iv) the relative rôles of physical and biotic environments in determining the distribution of each species.

Materials and Methods

The data reported here were gathered as part of a wider investigation of the epifauna of *Fucus serratus* at The Dorn, a National Nature Reserve in Strangford Lough, Co. Down. The area consists of several partially dammed shallow basins which provide a variety of physical and biological conditions within a comparatively restricted area. This variety was deliberately exploited for the present study, to obtain data on the bryozoan communities of *Fucus serratus* growing in a range of environments.

The major sample of plants, intended for statistical studies of Bryozoa distribution with respect to environment and competition, was collected in spring 1972. Sixty-five plants were harvested, five replicates being taken from each of 13 sites chosen for diversity of *Fucus* abundance and of current speed, relative water movement, and silt loads. Full details of the measurements of site environment and of plant characteristics are given in Boaden *et al.* (1975). For the present study the abundance of each species of bryozoan found was determined in a series of sample segments from each plant. Each plant was regarded as consisting of a series of Y-shaped dichotomies or segments whose position along the plant was specified by Y-values, from a basal Y1 to the distal Yn (the maximum value of *n* depending on the size and age of the *Fucus* plant). The size of each segment and the separate abundances of each bryozoan species on the two faces (one concave, one convex) of each segment along the longest frond of each plant were recorded. Replicate segments at the Y3 level (1–3 replicates) and at the Y5 level (1–7 replicates) were also examined to validate the use of the longest frond data. A total of 896 segments from this 1972 sample have been examined for the present report.

Statistical analysis of the 1972 data provided much information on the correlations between species abundances (Boaden *et al.*, 1975). Correlations are, however, not adequate evidence for causal relationships. We, therefore, conducted a further study in 1975. The history of behavioural interactions between colonies of Bryozoa can be established from microscopic study of their contact zones (Stebbing, 1973a, b). The 1975 sample was deliberately chosen to provide data of this type and comprised 15 plants from three environmentally diverse sites. A total of 430 segment-faces were examined for interactions within the epifauna. All interactions between Bryozoa were studied microscopically to identify the participant species, the nature and extent of the interaction, and the outcome. Since most Bryozoa breed in

British and Irish waters in summer (Ryland, 1970) the results of our study of a spring sample effectively summarize the outcome of a year's competition; this conclusion is supported by the results of our current longitudinal study of bryozoan population dynamics on *Fucus serratus* (unpubl. data). The results from this 1975 sample thus constitute data from a series of natural experiments for the measurement of spatial competition between species.

RESULTS

Four species of Bryozoa were particularly common on the *Fucus serratus* fronds examined. In order of abundance these species were *Flustrellidra hispida* (Fabricius), *Alcyonidium hirsutum* (Fleming), *Electra pilosa* (L.), and *Membranipora membranacea* (L.). A fifth species, *Celleporella hyalina* (L.), was also particularly abundant in the 1975 sample and has been included for some analyses here. Other bryozoan species present were too rare to warrant analyses of their occurrence.

SPECIES INTERACTIONS AT PLANT LEVEL

Size and bushiness are plant characteristics to which the five species studied here are differentially sensitive (O'Connor *et al.*, 1979). Such plant features could, therefore, serve as ecological isolating mechanisms. Their effectiveness in this respect was examined here by calculating the pattern of joint occurrences of species on the assumption of random distribution of the observed species counts over the available plants. The analysis was confined to the large (65 plants) 1972 sample. The numbers of plants carrying each combination of species was obtained by taking out the appropriate terms in the expansion of the distribution,

$$D(\mathrm{A, E, F, M}) = (p_\mathrm{A} + q_\mathrm{A})(p_\mathrm{E} + q_\mathrm{E})(p_\mathrm{F} + q_\mathrm{F})(p_\mathrm{M} + q_\mathrm{M})N,$$

where the subscripts refer to the four species in the sample, p and q are the proportions of all plants respectively colonized and not colonized by the species concerned, and N is the number of plants examined. Thus the term $p_\mathrm{A}\, p_\mathrm{E}\, q_\mathrm{F}\, q_\mathrm{M}\, N$ is the number of plants which would carry *Alcyonidium* and *Electra* but with the other two species absent, if the four species were occurring on the plants independently. This approach has been applied to a similar analysis of waterfowl distribution by Siegfried (1976). The results are summarized in Table I. The observed distribution of multiple species colonizations was very similar to that expected through independent settlement by each species.

This result is compatible with the differential sensitivity to plant characteristics noted above if any tendency by some species towards segregation is offset by a tendency for other species to associate on the same plants. We showed previously that certain species tended to occur together on the same segments of the *Fucus* plants, though the associations were weak and probably of little biological signific-

ance (Boaden *et al.*, 1975). Since association coefficients are subject to quadrat size effects (Krebs, 1977) we calculated new coefficients on the basis of the plant data just discussed and found (Table II) that *Flustrellidra* and *Electra* were the only two species statistically associated at plant level. It should be emphasized that this association need not be a direct response of the two species to each other: an independent response by each species to the one environmental factor would suffice.

TABLE I

Summary of segregation achieved by Bryozoa at the level of individual *Fucus* plants, with entries in the table showing the number of *Fucus* plants colonized by the number of bryozoan species stated, subject to the criterion of the left-hand column.

	Number of bryozoan species present		
Criterion	1	2	3
Irrespective of species identity	21	24	15
When *Alcyonidium* present	14	21	14
When *Electra* present	3	11	14
When *Flustrellidra* present	1	10	12
When *Membranipora* present	3	6	5

In addition two plants were colonized by all four species and three plants were unused by Bryozoa. An overall (d.f. = 4) χ^2 on these data yielded $\chi^2 = 0.52$, n.s., for the number of plants colonized by 0, 1, 2, 3, and 4 species of Bryozoa, irrespective of species identity. None of the individual species patterns deviate from random distributions. Data from the sixty-five 1972 plants.

TABLE II

Association coefficients between bryozoans on *Fucus* plants: association coefficients were calculated as $V = \sqrt{(a+b)(c+d)(a+c)(b+d)}$, where a is the number of plants colonized by both species, d the number of plants from which both species were absent, and b and c the number of plants colonized by each species in the absence of the other; 1972 data; * $\chi^2 = 4.10$, $P < 0.05$.

	Alcyonidium	*Electra*	*Flustrellidra*	*Membranipora*
Alcyonidium	1.000	−0.040	0.030	−0.097
Electra	−0.040	1.000	0.283*	−0.059
Flustrellidra	0.030	0.283*	1.000	−0.176
Membranipora	−0.097	−0.059	−0.176	1.000

Since there were no clear all-or-nothing associations apparent in the distribution of the bryozoans over the plants examined we investigated the possibility that the abundance of each species was influenced by the presence or absence of potential (or actual) bryozoan competitors. For each species in turn we calculated the mean abundance of the remaining three species in the presence and in the absence of the first species (Table III). The presence of *Alcyonidium* on a plant had no statistically significant effect on the mean abundance of the other three species, though the six-

fold reduction of *Membranipora* on plants colonized by *Alcyonidium* may be noted in the light of other results (below). On the other hand, *Flustrellidra* was significantly more abundant on plants with *Electra* present than on plants without *Electra*. *Electra* itself was, however, not significantly more numerous in the presence of *Flustrellidra*, though this may have been partly the result of the marked increase in the variability of its numbers under these conditions. A similar pattern but of opposite sign held for *Membranipora* and *Alcyonidium* with mutual reductions in numbers on plants carrying the other species, and with a marked increase in the relative variation of the *Membranipora* population when *Alcyonidium* was absent. *Membranipora* was also more variable in numbers where *Electra* was absent, and was more numerous when *Flustrellidra* was absent from the plants. These results suggest that *Electra* and

TABLE III

The influence of the presence of each bryozoan species on a plant on the abundance of other Bryozoa on that plant: abundance as cm^2 cover per segment face; 1972 data; t is Student's t-test result, with test modified for unequal variances where necessary; F is the logarithmic variance ratio of Lewontin (1966) and tests for differences in the coefficients of variation between absence and presence; in all tables $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

	Alcyonidium absent Mean ±SE	*Alcyonidium* present Mean ±SE	F	t
Electra	1.71 ± 0.78	0.82 ± 0.24	1.47	−1.09
Flustrellidra	1.36 ± 0.84	2.26 ± 0.95	1.72	0.71
Membranipora	0.72 ± 0.35	0.12 ± 0.06	3.69*	−1.69
Number of cases	14	51		
	Electra absent Mean ±SE	*Electra* present Mean ±SE	F	t
Alcyonidium	2.12 ± 0.59	1.89 ± 0.75	1.73	−0.24
Flustrellidra	0.47 ± 0.20	3.93 ± 1.60	1.24	2.15*
Membranipora	0.37 ± 0.16	0.10 ± 0.07	2.02*	−1.57
Number of cases	35	30		
	Flustrellidra absent Mean ±SE	*Flustrellidra* present Mean ±SE	F	t
Alcyonidium	1.90 ± 0.60	2.19 ± 0.75	1.37	0.30
Electra	0.68 ± 0.28	1.53 ± 0.46	2.91**	1.65
Membranipora	0.39 ± 0.14	0.03 ± 0.02	1.24	−2.46*
Number of cases	40	25		
	Membranipora absent Mean ±SE	*Membranipora* present Mean ±SE	F	t
Alcyonidium	2.54 ± 0.61	0.52 ± 0.16	1.28	−3.21**
Electra	1.10 ± 0.32	0.75 ± 0.33	1.28	−0.76
Flustrellidra	2.49 ± 1.00	0.87 ± 0.78	1.76	−1.28
Number of cases	48	17		

Flustrellidra had common requirements of the plants they utilized, whilst *Alcyonidium* and *Membranipora* had either opposite environmental requirements or mutually excluded each other from their plants; the latter also applies to *Membranipora* in relation to the *Electra – Flustrellidra* pair.

These patterns were investigated further by plotting the abundance of each species against the abundance of each other species occurring on the same plant. In this way only plants which were suitable for colonization by both species were considered and interactions between the two species were more likely to be revealed. In fact the results (Fig. 1) showed little evidence for direct interactions between *Alcyonidium* and any of the other species, nor between *Electra* and *Flustrellidra*. (There were too few data for the other species to warrant plotting.) There was, however, some indication that *Flustrellidra* and *Alcyonidium* each reached their greatest abundance only on plants where the other species was low in abundance, i.e. plants with both species present in low numbers were frequent but plants with large areas of Bryozoa had either *Flustrellidra* or *Alcyonidium* dominant (Fig. 1A).

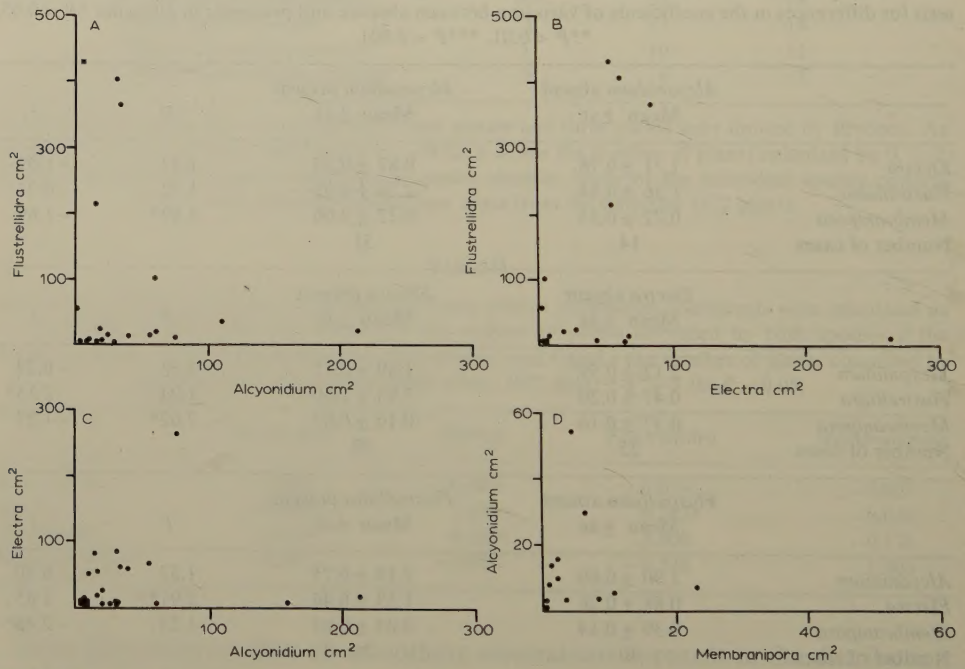

Fig. 1. Population size in relation to competition amongst the Bryozoa of *Fucus serratus*: each diagram shows joint abundances (total area per plant) of a species pair for plants with both present.

INTERACTIONS BETWEEN SPECIES AT SEGMENT LEVEL

We have already seen evidence for the interaction of species distributions at the level of individual plants (Table III) even though the overall use of plants was not

distinguishable from random colonization. In this section we wish to review the pairwise relationships of the five species at the level of individual segment-faces, i.e. after all potential isolating mechanisms examined above have had the opportunity to contribute to species segregation.

We have previously analysed the 1972 data in terms of association coefficients and of correlation coefficients (Boaden *et al.*, 1975). Association coefficients examine the tendency of pairs of species to co-occur on the same segment-face, irrespective of the abundance of each species. Correlation coefficients examine the tendency for the abundance of pairs of species to vary together. We found weak associations (<0.100) between *Alcyonidium* and both *Electra* and *Flustrellidra* and a stronger association (0.223) between *Electra* and *Flustrellidra*; *Membranipora* showed no associations of significance. All correlation coefficients were small, only that between *Electra* and *Flustrellidra* (0.069) attaining significance and this possibly only as a result of the very large sample size since the coefficient of determination showed less than 0.5% of the variation in abundances was involved. Table IV shows similar patterns in the 1975 sample. *Alcyonidium* was significantly associated with *Flustrellidra* which in turn was associated with *Electra*. *Membranipora* was not at all associated with the other three species (but in a tiny sample). *Celleporella* was positively associated with *Electra* but negatively with both *Flustrellidra* and *Alcyonidium*.

TABLE IV

Association coefficients between bryozoans in the 1975 *Fucus serratus* sample, measured at the level of individual segment-faces; $N = 430$.

	Alcyonidium	*Electra*	*Flustrellidra*	*Celleporella*
Alcyonidium	–	0.081	0.280***	−0.197***
Electra	0.081	–	0.178***	0.134**
Flustrellidra	0.280***	0.178***	–	−0.157**
Celleporella	−0.197***	0.134**	−0.157**	–

Table V presents the corresponding correlation coefficients. These show *Flustrellidra* and *Electra* numbers were correlated, as were those of *Flustrellidra* and *Alcyonidium*. *Celleporella* was less numerous where *Flustrellidra* was abundant and con-

TABLE V

Correlation coefficients between bryozoan pairs on *Fucus serratus*; data from 1975 sample, $N = 430$ segment faces.

	Alcyonidium	*Electra*	*Flustrellidra*	*Celleporella*
Alcyonidium	–	0.010	0.342***	−0.071
Electra	0.010	–	0.135**	−0.001
Flustrellidra	0.342***	0.135**	–	−0.096*
Celleporella	−0.072	−0.001	−0.096*	–

TABLE VI

The effect of the presence of a given bryozoan species on the abundance of other Bryozoa on the same part of the plant.

Reference species		*Alcyonidium*			
		Present	Absent		
Species affected	Year	Mean ± SE	Mean ± SE	*F*	*t*
Electra	1972	2.43 ± 0.68	0.77 ± 0.12	11.53***	2.40*
	1975	1.21 ± 0.31	0.68 ± 0.13	1.77	1.60
Flustrellidra	1972	3.60 ± 0.96	1.55 ± 0.29	3.92***	2.05*
	1975	14.78 ± 1.71	2.62 ± 0.38	6.32***	6.95***
Membranipora	1972	0.13 ± 0.06	0.23 ± 0.05	2.12***	1.33
Celleporella	1975	0.00	0.22 ± 0.05	–	2.50*
Reference species		*Electra*			
		Present	Absent		
Species affected	Year	Mean ± SE	Mean ± SE	*F*	*t*
Alcyonidium	1972	1.94 ± 0.44	2.04 ± 0.35	3.64***	0.18
	1975	1.42 ± 0.28	1.37 ± 0.26	1.83***	0.14
Flustrellidra	1972	6.67 ± 1.49	1.27 ± 0.28	5.27***	3.56***
	1975	8.27 ± 1.15	4.18 ± 0.60	1.82***	3.16**
Membranipora	1972	0.09 ± 0.04	0.22 ± 0.04	7.82***	2.34*
Celleporella	1975	0.27 ± 0.09	0.11 ± 0.03	3.87***	1.68
Reference species		*Flustrellidra*			
		Present	Absent		
Species affected	Year	Mean ± SE	Mean ± SE	*F*	*t*
Alcyonidium	1972	2.05 ± 0.46	2.03 ± 0.35	3.43***	0.04
	1975	2.64 ± 0.39	0.23 ± 0.05	51.24***	6.15***
Electra	1972	2.34 ± 0.55	1.02 ± 0.22	1.07	2.28*
	1975	1.35 ± 0.24	0.30 ± 0.05	18.87***	4.19***
Membranipora	1972	0.08 ± 0.04	0.22 ± 0.04	5.72***	2.24*
Celleporella	1975	0.07 ± 0.03	0.25 ± 0.06	5.04***	2.51*
Reference species		*Membranipora*			
		Present	Absent		
Species affected	Year	Mean ± SE	Mean ± SE	*F*	*t*
Alcyonidium	1972	0.23 ± 0.08	2.16 ± 0.33	241.55***	5.72***
Electra	1972	0.42 ± 0.23	1.27 ± 0.22	12.07***	2.67**
Flustrellidra	1972	0.81 ± 0.53	2.19 ± 0.36	6.08***	2.15*
Reference species		*Celleporella*			
		Present	Absent		
Species affected	Year	Mean ± SE	Mean ± SE	*F*	*t*
Alcyonidium	1975	0.00	1.56 ± 0.22	–	2.49*
Electra	1975	0.77 ± 0.17	0.81 ± 0.14	5.18***	0.15
Flustrellidra	1975	0.63 ± 0.21	6.13 ± 0.62	70.18***	8.41***

Note. A single 1975 instance of a plant colonized by *Membranipora* has been ignored here.

versely. Other pairings were not significantly correlated, despite the *Celleporella* results of Table IV. Thus, the two analyses imply that *Alcyonidium* and *Electra* were more numerous as *Flustrellidra* numbers increased, whilst *Celleporella* showed the opposite effect; *Celleporella* tended to be on the same faces as *Electra* and to avoid those with *Alcyonidium* but its numbers were unrelated to those of these two species.

The discrepancies between the results of Table IV and Table V proved to be due to non-linear relationships between the local densities of the various species. Table VI shows this by comparison of the abundances of each species in the presence and in the absence of each other species. *Flustrellidra* was significantly more numerous where *Alcyonidium* was present than where it was absent. *Alcyonidium* abundance was not related to *Flustrellidra's* presence or absence in 1972 but was less numerous where it was absent in the 1975 sample. *Electra* and *Alcyonidium* had no systematic relationships of this type except for *Electra's* depression in abundance in the absence of *Alcyonidium* in 1972. *Membranipora* abundance fell on *Alcyonidium's* entry and rose in its absence, but not significantly. *Celleporella* and *Alcyonidium* did not co-occur. *Electra* and *Flustrellidra* varied in abundance in parallel. *Electra* and *Membranipora* were negatively related, and *Electra* and *Celleporella* were not related. *Membranipora* and *Flustrellidra* were negatively related, as were *Celleporella* and *Flustrellidra*.

As the patterns just described were not necessarily due to causal correlations between species it was necessary to verify directly that competitive interactions between the species were present. In 1975 the incidence of such events was recorded. Broadly speaking, when two species of Bryozoa meet one of two responses occurs (Gordon, 1972; Stebbing, 1973a): growth in that direction may be halted and resumed in some other direction, or one species may simply overgrow the other, when then dies. Table VII shows our findings. *Electra* and *Flustrellidra* were the commonest species to co-occur on the same segment-face. Slightly more than half (57%) of all interactions between them ended in re-directed growth; of the remaining

TABLE VII

Interactions between Bryozoa on *Fucus serratus*.

Interaction	Number of faces with both species	Number of interactions	Interactions per face	Overgrowth per interaction (%)
Flustrellidra overgrowing *Electra*	86	96	1.12	1.38
Electra overgrowing *Flustrellidra*	86	4	0.05	1.00
Flustrellidra and *Electra* meet	86	130	1.51	–
Flustrellidra overgrowing *Alcyonidium*	75	36	0.48	1.20
Alcyonidium overgrowing *Flustrellidra*	75	19	0.25	1.00
Flustrellidra and *Alcyonidium* meet	75	275	3.67	–
Alcyonidium overgrowing *Electra*	41	0	0.00	–
Electra overgrowing *Alcyonidium*	41	0	0.00	–
Alcyonidium and *Electra* meet	41	20	0.50	–

cases *Flustrellidra* emerged victorious in 96%. Note, however, the relatively small extent of the overgrowth, an average of only 1.38% of the *Electra* colony overgrown being lost, although this was still larger than losses in the opposite direction (when they occurred). *Flustrellidra* and *Alcyonidium* also co-occurred frequently and had an even greater frequency of interactions. Here, however, some 83% took the form of re-directed growth, this high percentage possibly being linked with more evenly matched competitive ability, as *Alcyonidium* managed to win a third of the overgrowth contests. The extent of actual overgrowth was again small, at 1.0–1.2%. *Electra* co-occurred with *Alcyonidium* in 41 cases, all of them resulting in the cessation of growth at the point of contact. In terms of total interactions *Alcyonidium* and *Flustrellidra* came most frequently into conflict, with 4.4 interactions per face, then came *Flustrellidra* and *Electra* with 2.7 interactions per face, and finally *Alcyonidium* with *Electra* with 0.5 interactions per jointly colonized face. No other species pairs were detected in interactions of the types described, possibly because of the small numbers of joint occurrences (maximum 24 for *Celleporella* and *Electra*). In addition to the cases described 13 cases of *Electra* settling on existing *Flustrellidra* colonies were recorded and one further case of its settlement on *Alcyonidium*.

The longitudinal distribution of interactions is presented in Fig. 2. There were no significant differences between the distributions of the different types of interactions and they have, therefore, been pooled for each species-pair here. The distributions of interactions between the members of each of the three species-pairs

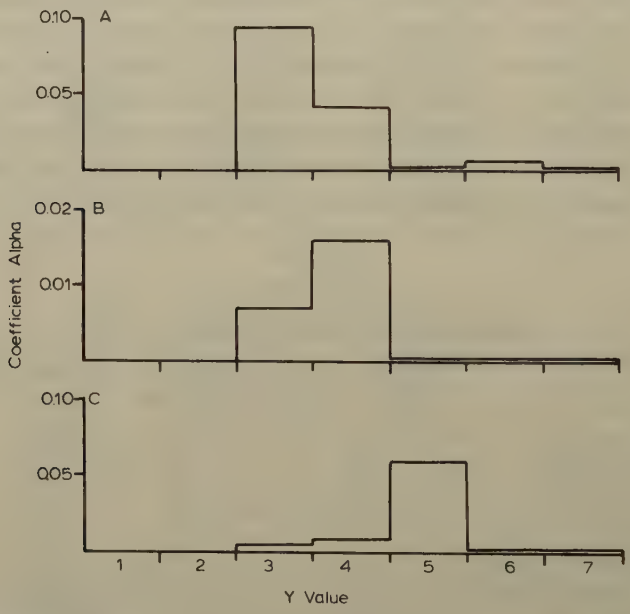

Fig. 2. The distribution along *Fucus serratus* of the interactions between *Flustrellidra* and *Alcyonidium* (A), *Flustrellidra* and *Electra* (B), and *Alcyonidium* and *Electra* (C): all interaction types are included (see text).

considered were all rather similar, each with the maximum frequencies in the Y3–Y5 region (Fig. 2). These interactions essentially followed the joint-occurrence probabilities calculated for species pairs from data on individual species distributions and thus did not reflect some local concentration of interactions.

MULTI-SPECIES UTILIZATION OF SEGMENTS

Competition is usually assumed to be an organizing force within communities but often the assumption lacks any real evidence. We showed previously that the distribution of Bryozoa within our 1972 sample satisfied some predictions of competition theory (O'Connor *et al.*, 1975) but, in view of a recent paper by Ricklefs & Travis (in press) who found that even an apparently well-organized community may not be distinguishable from a random assemblage of species, we examine here the distribution of multi-species occurrences at the level of the individual segment-faces of the seaweed.

TABLE VIII

Comparison of observed multi-species occurrence on segment faces on *Fucus serratus* with the random distributions expected from the relative frequency of individual Bryozoa species.

Number of species present N	Frequency of occurrence in 1972			Frequency of occurrence in 1975			Relative frequency of N species	
	Observed	Expected	Deviation	Observed	Expected	Deviation	1972	1975
0	473	444.4	+28.6	135	101.4	+33.6	52.8	31.4
1	301	348.5	−47.5	126	187.9	−61.9	33.6	29.3
2	102	92.8	+ 9.2	134	113.1	+21.9	11.4	31.4
3	20	10.3	+ 9.7	35	27.6	+ 7.4	2.2	8.1
	$\chi^2 = 18.36$, $P < 0.01$			$\chi^2 = 37.37$, $P < 0.001$				

Table VIII compares the frequencies of multi-species colonization observed against those occurring on the basis of independent utilization of the available dichotomies by the bryozoan species involved. The analysis is thus an exact analogue of that of Table I but at the level of segment-faces rather than of plants. In both samples the observed distributions were significantly non-random: there were more faces uncolonized by any bryozoan than expected by chance and there were markedly fewer instances than expected of only one species represented on a face. Such results imply that species were avoiding certain parts of the plants (or of some plants) and crowding together on other faces. Comparison of the relative frequencies of faces with 0, 1, 2, and more than 2 Bryozoa present in the two samples shows that nearly a third of the faces were totally uncolonized in 1975 but over half (52.8%) in 1972. This difference reflects the different purposes of collection of the two samples, since the 1975 sample was especially chosen for a study of species interactions. The proportions of one-species-only cases were similar in the two years, but there were proportionately more multi-species cases in 1975, again reflecting the purpose of its collection.

Although Table VIII shows a deficit of single species occurrences a detailed examination showed between-species differences on this point. In 1972 *Membranipora* occurred alone on 41 faces, against the expected value of 32. *Celleporella* occurred alone about as frequently as expected in 1975 (14 against the expected 12.4). *Celleporella* also occurred as a pair with *Electra* more often than expected (21 against 6.1). Finally *Electra* and *Flustrellidra* occurred jointly more often than expected both in 1972 (25 cases against 13.5 expected) and in 1975 (51 against 45.9), and the pair also occurred in a triplet with *Alcyonidium* surprisingly often (1972: 18 against 4.9; 1975: 32 against 14.5). The pattern of Table VIII was thus in part due to the segregation of *Membranipora* from the other species and in part due to the joint association of *Electra* and *Flustrellidra* and of *Electra* with other species.

TABLE IX

Competition coefficients for Bryozoa sampled on *Fucus serratus* in 1972.

	Species affecting			
Species affected	*Alcyonidium*	*Electra*	*Flustrellidra*	*Membranipora*
Alcyonidium	–	0.025	0.021	0.001
Electra	0.076	–	0.236	0.001
Flustrellidra	0.016	0.059	–	0.002
Membranipora	0.043	0.014	0.076	–

If several species can congregate on the same parts of the plant then realized competition must be low. Table IX confirms this by presenting competition coefficients calculated from a modification of the formula presented by Ricklefs (1973, p. 518), viz.

$$\alpha_{ji} = \frac{\sum_h A_{ih} A_{jh}}{\sum_h A_{ih}^2},$$

where α_{ji} refers to the competitive effect of species j on species i, h is some partition of resource space, here segment-faces, and A is the area covered by the species concerned. Note that slight changes would enter here if zooid densities were used, since these may differ in space requirements between species. The results show, however, that interspecific competition was in all cases quite low relative to intraspecific competition ($\alpha = 1$), although there remain asymmetries. Thus *Flustrellidra* had a more severe effect on *Electra* than *Electra* had on it, and had a very slightly more severe effect on *Alcyonidium* than held conversely. These effects may be compared against the direct observations of interactions between these species (Table VII), since the two data sets are completely independent. *Alcyonidium* and *Electra* also showed asymmetries in favour of the former. *Membranipora* was the loser against the other three species, in keeping with the results of the previous paragraph and in

keeping with its virtual absence from the intensely competitive 1975 sample. This point is investigated further in Fig. 3 in which the variation in competition coefficients with position along the fronds is presented. This shows that *Alcyonidium*, *Electra*, and *Flustrellidra* peaked in competitive efficiency against *Membranipora* at different points along the frond, so that no point within the central zone of the plant was competition-free for *Membranipora* colonization. The coefficients were all rather low, although this will have been offset by the higher densities of these species when compared with *Membranipora* (see Table I of O'Connor *et al.*, 1979). The coefficients measuring the effects of *Membranipora* on the other three species, however, were even lower (<0.015 in all cases).

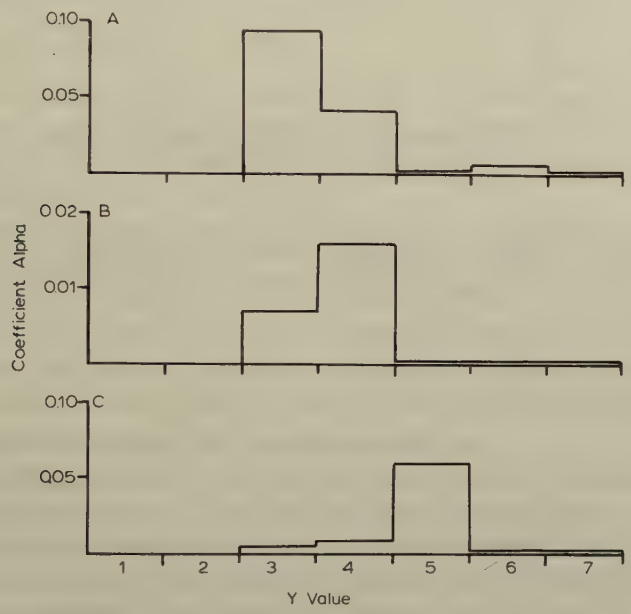

Fig. 3. Intensity of competition between *Membranipora* and other bryozoans along *Fucus serratus*: competition measured as the alpha coefficient (Levins, 1968) for the effects on *Membranipora* of *Alcyonidium* (A), *Electra* (B), and *Flustrellidra* (C).

Fig. 4 shows a related analysis for competition between *Flustrellidra* and *Alcyonidium*. This suggests that *Flustrellidra* was competitively superior around Y3 but inferior more distally, at Y6. This may well be related to the niche shift with turbulence previously reported for this species (O'Connor *et al.*, 1979). *Alcyonidium* is able to maintain high densities around the Y5 and Y6 levels of plants in quiet waters whereas the density of *Flustrellidra* drops sharply under these conditions.

Similar analyses for longitudinal variation in competitive ability for the *Alcyonidium–Electra* and *Electra–Flustrellidra* pairs gave no evidence of such patterns.

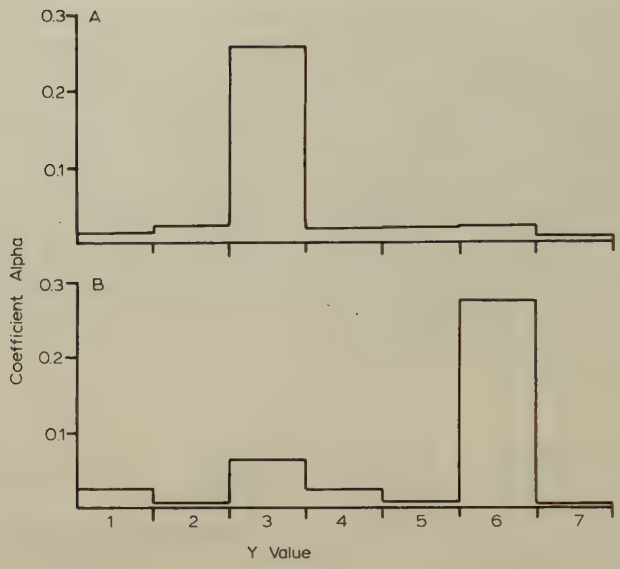

Fig. 4. Reversal of competitive superiority in *Flustrellidra–Alcyonidium* interactions along *Fucus serratus* fronds: competitive ability assessed as alpha coefficients (Levins, 1968) for the effect of *Flustrellidra* on *Alcyonidium* (A) and the effect of *Alcyonidium* on *Flustrellidra* (B).

MULTIPLE REGRESSION ANALYSES

An attempt was made to separate the effects of the different variables considered above by conducting multiple regression analyses on species abundance data. The gross effects of environmental conditions unsuitable for each species were reduced by considering only segments actually colonized by the species concerned. Dependent variables were logarithmically transformed for normality and regressed in step-up mode on the areal abundance of the other species and on plant length and segment area, length, breadth, and position on plant (Y-value). Units used in the equations below are mm and mm^2, as appropriate.

For *Alcyonidium* the equation obtained was

$$LA = 0.0100YA - 0.0014F - 0.0919 \qquad 100R^2 = 19.2,$$

where *LA* codes for logarithmic transformation of *Alcyonidium*, *YA* is the segment area and *F* is *Flustrellidra* area. Thus *Alcyonidium* tended to be more abundant on the larger segments of the *Fucus* plants and to be scarcer where *Flustrellidra* was also present on the segment. About one-fifth (19.2%) of the variance in *Alcyonidium* is accounted for by this regression.

For *Electra* the equation obtained was

$$LE = 0.0094YA + 0.0443 \qquad 100R^2 = 23.5,$$

Thus *Electra* also colonized larger segments (or achieved greater colony size thereon) but was not influenced by the abundance of other species.

For *Flustrellidra* the equation obtained was

$$LF = 0.0976\,YL - 0.1251\,YV + 0.8838 \qquad 100R^2 = 11.8,$$

where YL is the segment length and YV is the Y-value of the segment. The equation shows that *Flustrellidra* was more abundant on long segments of the plant than on short segments and also tended to decrease towards the apical end of the plant. The regression accounted for only 11.8% of the variance in *Flustrellidra* numbers, however, so the correlates are not of major importance.

For *Membranipora* the regression yielded

$$LM = 0.3978\,YB - 1.0379 \qquad 100R^2 = 39.7,$$

showing that nearly 40% of the variation in *Membranipora* numbers was correlated with the width of the segment on which it occurred.

For *Celleporella* the analysis was conducted without logarithmic transformation and using all segments and yielded

$$C = -0.146PW + 0.539\,YA - 0.592PL + 0.488 \qquad 100R^2 = 4.2,$$

where PW is plant weight (g) and PL is plant length (cm). The regression shows the tendency to colonize small *Fucus* plants that we have described elsewhere (O'Connor *et al.*, 1979), with an additional tendency to use the larger segments within such plants. The proportion of variance explained by the regression is very low, however, so other factors than those measured here must be important.

An interesting point about all five regressions is their inclusion of a segment dimension with positive sign. That is, for all five species abundance was correlated with the size of the segment colonized. Since the length, breadth, and area of *Fucus serratus* segments are mutually correlated (Boaden *et al.*, 1975) the results are consistent with segment area being the limiting resource for these bryozoan populations. Separate regressions of the percentage cover of each segment by each species on segment area in the two years yielded significant negative correlations in the cases of *Flustrellidra* ($r = -0.190$, $P < 0.01$ in 1972) and of *Electra* ($r = -0.259$, $P < 0.05$ in 1975) but not for the other species. This implies that the largest segments might be relatively unsaturated by *Flustrellidra* and by *Electra* in these years, species otherwise maintaining constant (and perhaps species-specific) densities over the available space.

Discussion

The question of how available resources are partitioned between competing species has attracted considerable attention in recent years. Several studies have

suggested that in competition dominated environments there can be no more species than there are separate resources (MacArthur & Levins, 1964; MacArthur & Wilson, 1967; Levins, 1968). Paine (1971) points out, however, that predation tends to reverse the action of competition which there would otherwise be between species sharing a particular resource. Thus, given a suitable predation regime species can co-exist within the resource. The relative importance of competition and predation in the allocation of space in rocky intertidal habitats has been discussed in a number of papers (e.g. Dayton, 1971, 1973; Paine, 1971, 1974; Connell, 1972; Menge, 1976). At present since there is little evidence concerning the impact of predation on algal epifaunas (see, however, Seed, 1975; Ryland, 1976) its possible rôle in counteracting the effects of competition cannot be assessed. Our Dorn data, however, allow some assessment of the extent and effects of interspecific competition and suggest various other mechanisms by which this may have been minimized within the algal epifauna.

The distribution of several non-bryozoan species of The Dorn *Fucus serratus* community is known to be intimately affected by competitive spatial interactions (O'Connor *et al.*, 1975; Boaden *et al.*, 1976) and the present results suggest the same pattern for the Bryozoa. Gordon (1972) lists the types of response that can occur when different species of Bryozoa meet, namely: cessation of growth, overgrowth (thin colonies being overgrown more frequently by thicker colonies than vice versa), and stolonic overgrowth. Comparison of data from The Dorn (Table VII here, and also Seed & Boaden, 1977) with that from southwest England and other parts of the British Isles (Stebbing, 1973 a, b) shows a close similarity in the outcome of intraspecific competition.

Electra was frequently overgrown by other species but the most common response was for growth to halt at the site of opposition and to be re-directed elsewhere. Such a response obviously reduces the intensity of local spatial competition and must be important in permitting the frequent occurrence of the *Electra–Flustrellidra* pair (alone and in trio with *Alcyonidium*) noted above. *Electra* displays several adaptations which may be associated with its persistence in a competitive environment; these include spines to inhibit overgrowth (Stebbing, 1973a), a relatively rapid growth rate, and an ability to orient towards the younger, less encrusted, parts of host plants (Ryland & Stebbing, 1971). It is significant in respect of this last trait that *Electra* was second only to *Membranipora* in the dependence of its numbers on segment area in the multiple regression analyses whilst at the same time its intensity of use (as percentage of segment covered) decreased with increase in segment area. These traits allow *Electra* to become an important and sometimes dominant component of the *Fucus* epifauna.

Flustrellidra was clearly competitively the most superior of the species studied here (Tables VII, VIII). This goes some way towards explaining its numerical dominance which, however, depends in part on the local environment or microenvironment (O'Connor *et al.*, 1979). The presence or absence of *Flustrellidra* on a

plant had little or no effect on the abundance of *Alcyonidium* on that plant although there was a significant positive association between its occurrence and that of *Electra* with regard to the particular plants utilized (Tables II, III). Both the presence and the abundance of *Flustrellidra* were positively associated with those of both *Alcyonidium* and *Electra* (Tables IV, V, VI), but the multiple regression analyses suggest that these associations were the outcome of shared (or partially shared) environmental requirements at plant level.

Flustrellidra numbers were lower in the presence of *Membranipora* than in its absence. This effect was reciprocal indicating that the pattern was associated with differential responses to environment rather than directly with competitive interaction. These two species are those whose numbers were most sensitive to the environmental differences between sites (O'Connor *et al.*, 1979); such sensitivity could itself have evolved in response to intraspecific competition. Similarly, Stebbing (1971) has shown that potentially competing pairs of bryozoan species on *Flustra foliacea* occupy quite different micro-habitats. Such differences are again evident in the interaction between *Flustrellidra* and *Alcyonidium* (Fig. 4), the species' mutual competitive ability being reversed with distance along the frond. This is to be compared with the shift in niche position (towards the basal part of the frond) shown by *Alcyonidium* as turbulence increases (O'Connor *et al.*, 1979). Local competitive superiority may also underlie the relationship of the two species (Fig. 1A) of concurrence of low density populations of both species but not of high density populations; that is, when either *Flustrellidra* or *Alcyonidium* was abundant the other species was absent or scarce.

Alcyonidium emerges from our analyses as a relatively ubiquitous species occurring in moderate numbers over a wide range of environmental conditions (Boaden *et al.*, 1975; O'Connor *et al.*, 1979). It is possibly less subject to competitive exclusion than some species and, given suitable conditions, can hold its own in competition with other bryozoan species even including *Flustrellidra* (see above). Nevertheless, multiple regression analysis indicated that the extent of *Alcyonidium* colonies was depressed with increase in *Flustrellidra* density. It is probable that this and other results comparing *Alcyonidium* with other species (e.g. Table VI) reflect differential sensitivity to the physical environment. Thus, although *Alcyonidium* shares various environmental requirements with *Electra* and *Flustrellidra* its sensitivity to those factors was comparatively less (O'Connor *et al.*, 1979). This relative insensitivity or lack of attunement allows the more ubiquitous distribution of *Alcyonidium* and explains the otherwise unexpectedly frequent occurrence of the *Alcyonidium–Electra–Flustrellidra* species triplet. It should also be borne in mind that our results deal with *Alcyonidium hirsutum* (Fleming) *sensu latum* and that this taxon, electrophoretically at least, may be differentiated into at least four smaller taxa (Thorpe & Ryland, 1979).

Membranipora differs from the other bryozoan species studied at The Dorn in both sensitivity to turbulence and to plant silt load, occurring predominantly in quiet silt-free waters (O'Connor *et al.*, 1979). This largely explains the comparative

distribution and abundance noted above, although interspecific competition is certainly a contributory factor. The relatively thin mat-like growth form of *Membranipora* colonies is particularly prone to overgrowth (Gordon, 1972; Stebbing, 1973a) and *Membranipora's* three main bryozoan rivals are each competitively superior at different positions along the plant frond (Fig. 3). *Membranipora* populations would, therefore, suffer disastrously from single species competition and from the more severe effects of diffuse competition (MacArthur, 1972; O'Connor *et al.*, 1975) were they concurrently distributed with other Bryozoa. *Membranipora*, however, colonizes (or differentially survives on) a different spectrum of plants according to whether other bryozoans are abundant or scarce (O'Connor *et al.*, 1979 and Table III here) and, as stated, is favoured in "quiet" areas at The Dorn (which are relatively free from competition). Thus the distribution of *Membranipora* may be interpreted in terms of competitive exclusion. We suggest that although the *Membranipora* growth form may be particularly suited to broad segments, the association of 40% of the variation of *Membranipora* abundance with frond breadth shown by the multiple regression analysis may also be a reflection of poor competitive ability where space is at a premium.

Celleporella, as shown in our previous paper, uses shorter, less bushy, plants than other species. Our present analyses, based as they are on rather few samples, provide little evidence of which other factors may be important, excluding minor contributions from segment area.

Segment dimensions (area, length or breadth) enter significantly into all of our multiple regressions. This contributes towards the explanation of the previously discovered correlations between the area of a segment and the number and diversity index of its encrusting Bryozoa (O'Connor *et al.*, 1979).

The multiple regression analyses suggest that, of the species concerned, interspecific competition is only effectively realized between *Alcyonidium* and *Flustrellidra*. This is probably because these two species are brought together by shared environmental requirements. The low size of the competition coefficients indicates, however, that intra- rather than inter-specific competition must be dominant. It could well be that sensitivity to segment dimensions is really an expression of intraspecific spatial competition.

Interesting differences are revealed when the pattern of multi-species occurrence at plant level (Table I) is compared with that at segment face level (Table VIII). The former could not be distinguished from independent distribution of species except for the association of *Electra* and *Flustrellidra*. Segment face occurrence, however, showed too many non-colonized faces and too few single-species-colonized faces for species distribution to be independent, largely due to a segregation of *Membranipora* from the other species and to a concurrence of *Electra* and *Flustrellidra*. This implies that spatial segregation of Bryozoa had occurred at segment rather than at plant level. It is of course already well known (Ryland, 1959; Stebbing, 1972; Seed, 1975) that some species settle selectively on the youngest parts of fronds thereby

reducing both inter- and intraspecific competition (again at segment rather than plant level).

Many of the important species within epifaunal communities are filter-feeders and it seems possible, therefore, that there will be some competition for particular food. Ryland (1975), e.g. concluded that the majority of bryozoans on a New Zealand seashore were probably consuming particles within the same size range. Food selection by filter-feeding organisms usually occurs, however, within broad limits (Jørgensen, 1966) and is thus unlikely to provide a segregation mechanism which would effectively reduce competition. In any case the abundance of filter-feeders at The Dorn, both on *Fucus* and in other habitats, suggests that food is not a limiting factor in this area. Moreover, O'Connor & Lamont (1978) have shown experimentally that the provision of extra settlement space in sites of already abundant *Spirobis* populations led to a further increase in population, implying that space, rather than food, was the limiting factor for these species which, in turn, have been shown to compete with Bryozoa for space on *Fucus serratus* plants at The Dorn (unpubl. data) and elsewhere (Stebbing, 1973a).

In general it seems that bryozoans fare badly in direct competition with other taxa. On *Fucus serratus* they can outcompete and overgrow stolons of the hydroid *Dynamena* (Stebbing 1973a; Seed & Boaden, 1977) and the solitary tubes of spirorbids (O'Connor & Lamont, 1978) but suffer badly from smothering by sponges and ascidians which may be aided by chemical secretions (Ryland, 1976). According to our results, however, direct competition, at least between established bryozoan colonies, is the exception rather than the rule. The resource of space is effectively partitioned amongst bryozoans by the array and range of factors to which each species is sensitive. This sensitvity may be recognized through the species distribution pattern as expressed at site, plant or within plant level. Ultimately, as some preferenda overlap, because a certain element of opportunism exists, and because some microhabitats are particularly advantageous, resource partitioning may fail. A proportion of each population concerned will then be in direct interspecific conflict. The outcome of this competition depends on a complex of factors which includes behavioural interactions such as overgrowth as well as the relative attunement of the species to the prevalent environmental conditions at the site of conflict.

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SPATIAL RELATIONSHIPS AND SOME STRUCTURING PROCESSES IN BENTHIC INTERTIDAL ANIMAL COMMUNITIES

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Abstract: Species diversity and the occupation of primary and secondary space was examined in a benthic intertidal habitat. Replicate climax communities on experimental blocks (over 3 yr old) were compared with short-term (3-month) collections of settling larvae. Rather than occupying free primary space, perennial species occupied secondary (epizooic) space by overgrowth (in colonial bryozoans) and by preferential settlement (studied in the solitary tubeworm *Spirorbis*). The clumped distributions of animals and the occupation of secondary space while free primary space remained suggests that primary space was not limiting during all periods of the year, as is frequently assumed for sessile communities. Differences in patterns of diversity were observed for colonial and solitary animals. Although there were comparable numbers of colonial bryozoan species on each climax block, there was little overlap in species composition among blocks. While solitary animals were consistently present and showed reduced diversity, high diversity was maintained in colonial forms with similar species apparently substituting for each other on different blocks. These collections of animals are suggestive of multiple climax states and were identified as different communities. Those species initially occupying free space seemed to affect secondary colonization of the area, presumably by attracting or excluding settling larvae or spreading species. Seasonally abundant species, competitively superior to non-seasonal species, may produce selection pressures favouring the occupation of secondary space by perennial animals.

INTRODUCTION

The processes that generate particular patterns of species diversity among communities of immobile organisms are often strongly linked to species patterns in the occupation of space. Well-studied intertidal barnacle–mussel communities are believed to rely on predation and disturbance to create new patches of bare substratum that allow new species to enter (Paine, 1974). The argument is that suitable, hard, primary surfaces for growth are in short supply relative to the demand by all species (Connell, 1961a, b; Paine, 1966, 1971, 1974; Dayton, 1971). Heavy occupation of primary space in established or "climax" communities, low species diversity and a substantial frequency of overgrowth among animals are usually regarded as support for this argument (Jackson, 1977).

In contrast, encrusting communities associated with small boulders or other discrete patches of substratum are often compositionally diverse even in the apparent absence of disturbance. Perhaps because of insufficient study, species diversity has

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not been clearly related to density of space utilization or frequency of overgrowth. Furthermore, in contrast to other intertidal organisms, the spatial distributions of encrusting species have not been well correlated with other aspects of their biology. For example, colonial and solitary growth forms, comprising most encrusting communities, differ in their potential for space occupation and, therefore, in their impact on the benthic community. Many colonial animals are able to reproduce asexually, via budding, fission or gemmules, as well as sexually (Jackson, 1977), and so can grow to very large sizes. Solitary animals reach a predictable adult size determined by physiological factors and generally occupy much smaller portions of the substratum than do colonial animals. For these reasons, colonial animals when compared with solitary animals, should behave differently in the initial occupation of the substratum (settling) and in the maintenance of their position in the community.

The benthic invertebrate community on the bottom of boulders represents a particular group of intertidal invertebrates. This structurally simple habitat is protected from desiccation and heavy wave action and, because of low light levels, colonizers do not compete with algae which may grow quickly and smother juvenile animals on more well-lighted surfaces. To determine whether community organization could best be explained by competition for space, as assumed for other habitats, we examined spatial patterning and diversity on the bottoms of small rock islands. Concrete blocks, representing rock surfaces, from two age classes were examined to compare settling communities with those already established. Organizational processes responsible for inequitable distributions of animals within and among blocks were studied by comparing replicate block communities of the same age.

Materials and Methods

The area studied was a rocky beach on Diana Island in Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. The beach faces into a channel between two islands and has no open sea angle. Boulders rest on a rock surface rather than on sand and the algal and faunal communities are extensive.

Five 900-cm^2 concrete blocks were placed within a few metres of each other on the beach in July, 1974. Blocks were collected from 1.0 and 1.3 m above the zero datum level at various times during the winter of 1977–1978 and these blocks formed the basis of the study of the climax community. New blocks were placed on the beach in November, 1977, <1 m from each other at 1 m above zero datum. The ages, treatments, and collecting dates of the Diana Island blocks are shown in Table I.

The collecting blocks used were standard $30 \times 30 \times 5$ cm concrete patio blocks. When returned to the laboratory, the plates were stored in 95% alcohol for at least 24 h prior to drying. No further preservation was needed as all structures remained intact and most animals could be readily identified. Most of the invertebrates on the

blocks possessed calcareous skeletons which remained intact after the animal tissue dried.

TABLE I

Ages and treatments of the Diana Island study blocks.

Block	Date set out	Treatment	Date collected	Age
1	July, 1974		Nov., 1977	3 yr 4 months
2	July, 1974		Nov., 1977	3 yr 4 months
3	July, 1974		Feb., 1978	3 yr 7 months
4	July, 1974	All animals were scraped off half of the block in November, 1977	March, 1978	3 yr 8 months
5	July, 1974	All animals were scraped off half of the block in November, 1977	March, 1978	3 yr 8 months
6	Nov., 1977		March, 1978	3 months
7	Nov., 1977		March, 1978	3 months

A clear plastic grid was marked in 841 1-cm^2 quadrats for sampling. To reduce any biases due to "edge effects" 0.5 cm was left outside the quadrats on the block edges. The number of quadrats to be microscopically examined at a magnification of $\times 50$ was determined from a species-area curve constructed for the blocks: 50 random quadrats (95% of all species) were sampled on each block. The few organisms not identifiable at this magnification were ignored.

Within each quadrat, the surface area and type of substratum were recorded for each species and the number of individuals was noted for solitary species. Because some organisms can grow on top of others without harm to either species, there is a potential for $>100\%$ occupation of the surface area within a quadrat.

Identification of animals was carried to species level whenever possible, but for some species of bryozoans only arbitrary identification was made (Species A, Species B, etc.). Distinctions were made between adult and juvenile *Spirorbis spirillum*[1] worms; any worm smaller than the largest specimen on a 3-month old block was identified as a juvenile.

[1] Authorities for all scientific names used herein are as cited in Smith & Carlton (1975).

Results

COMPOSITION AND DIVERSITY AT CLIMAX

Twenty-seven species of perennial sessile invertebrates were encountered in a sample of 150 1-cm^2 quadrats from three climax blocks. The majority of the species found were colonial bryozoans; only 4 of the 27 species were solitary (2 tubeworms, a barnacle, a sessile mollusc). These colonial species have a high potential for occupying space – although individual bryozoans were very small, a colony sometimes covered several cm^2 of rock surface, an area much larger than that taken up by any of the solitary species.

Bryozoans, which comprised as much as 88% of the occupied surface, were a notably diverse group. Twenty-three species were represented, only two of which occurred on all three climax blocks. Six of the species occurred on two of the three blocks while 15 species were sampled on only one climax block. In contrast four species of solitary animals were present in the climax community and three of these were on all blocks. Sorensen's coefficient was used (Brower & Zar, 1977) to calculate community similarity between the three possible pairs of blocks. Blocks 1 and 3 were the most similar (0.526) but even this value is not especially high. Other calculated coefficients were 0.333 for Blocks 1 and 2, and 0.261 for Blocks 2 and 3.

On the other hand, if bryozoans were considered collectively the blocks were very similar in composition. The pie diagrams (Fig. 1) show this crude similarity. Each block contained similar numbers (9, 10, and 14) of bryozoan species and although the absolute proportions of all species shown were not the same among blocks, there was the same trend in the domination of space on each block. Bryozoans occupied the largest relative proportion of the area, followed by *Spirorbis*, *Serpula vermicularis* (a sessile polychaete), and then the sedentary mollusc *Dendropoma lituella*.

The pie diagrams also show that considerable disparity existed in the areas occupied by each group of animals and in the amounts of unoccupied space encountered among blocks. Although epizoic overgrowth provides a potential for >100% occupation of the substratum, this state was not approached on any of the blocks, even though many animals were observed growing on other species. Not only was there a surprisingly large amount of primary space available in the climax community, but the amount of open space varied widely from block to block. Nonetheless, each block possessed a similar fauna.

Given the widely held assumption that primary space is limiting in intertidal communities, we expected the number of species to be closely tied to the amount of space occupied by these organisms, but the number of species present on a single block had a narrow range (from 48 to 66% of the total number of species) when compared with the range in area occupied (from 15 to 66%). The number of species present does not appear related to the area of block occupied by animals.

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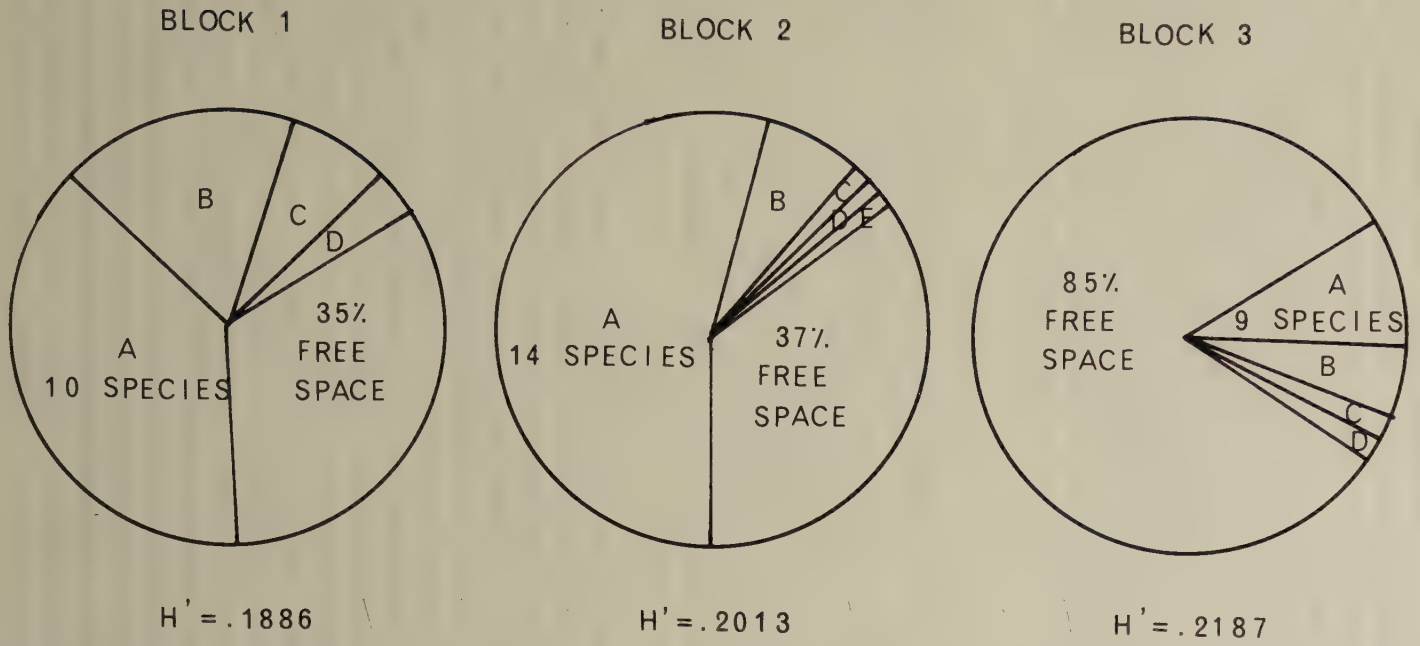

Fig. 1. An illustration of the proportions of space occupied by each group of organisms on the three climax community blocks: *H'*, the Shannon–Weiner index, indicates the diversity calculated for each block; A, Bryozoa; B, *Spirorbis spirillum*; C, *Serpula vermicularis*; D, *Dendropoma lituella*; E, *Balanus glandula*.

Species diversity can be measured among the climax blocks by weighting each species by its relative coverage. We used the Shannon–Weiner index (Pielou, 1975) to calculate the diversity of the climax community blocks. In a climax community, competition and other negative interactions usually reduce diversity through preemption of resources by a few superior competitors. If primary space were limiting in our communities, then diversity should be lowest on blocks which were most fully occupied and superior competitors should predominate. Fig. 1 shows the amount of unoccupied space in comparison with the calculated H' values. Generally the index is lower when there was less space available, but the large variation in the amount of unoccupied space is not reflected by major changes in H'.

The pie diagrams indicate that large and variable regions of bare space existed within the climax community. An analysis of variance (Table II) of the amount of

TABLE II

One-way analysis of the variance of the amount of space occupied per quadrat in the climax community: $n = 175$.

Source	d.f.	Sum of squares	Mean square	F	Significance
Among blocks	3	7927.04	2642.35	6.98	$P < 0.001$
Within blocks	171	64691.17	378.31		
Total	174	72618.21			

Components of variance: variance among blocks = 12.3%; variance within blocks = 87.7%.

primary space occupied per quadrat showed, as expected, that the blocks differed significantly. Calculated components of variance indicated, however, that most of the observed variance in the amount of open primary space (88%) was contained within the blocks at the quadrat level. Hence, examination of the distribution of animals at this latter level rather than among blocks should prove more useful in disclosing process that affected community organization.

Under the usual assumption that primary space limits success of most encrusting species, wide variation in the amount of space occupied at the quadrat level implies a potentially wide range of possible spatial relationships among species. For example, with less free primary space available (e.g., Block 1), species should be more competitively constrained in their use of the remaining primary space than when space is abundant (e.g., Block 3). Under the latter conditions, the distribution of organisms should more closely resemble a random distribution than when space is scarce and competition is fierce. We examined this hypothesis by comparing the distribution of numbers of species per quadrat with a Poisson distribution and found that the distribution of species among quadrats was highly clumped regardless of the amount of free primary space available.

Block 1, $\chi^2 = 15.46$, d.f. = 5, $P < 0.05$, $s/\bar{x} = 3.70$
Block 2, $\chi^2 = 15.22$, d.f. = 5, $P < 0.05$, $s/\bar{x} = 3.46$
Block 3, $\chi^2 = 14.78$, d.f. = 5, $P < 0.05$, $s/\bar{x} = 3.64$

Either free primary space, in contrast to current assumptions, is not a resource that most of these climax community species require or they are not capable of exploiting this space if it becomes available during winter. By the former hypothesis, climax species are clumped because there is adaptive value in settling and growing in close proximity to others rather than alone on open primary space. By the alternative and usual hypothesis, community patterns in the use of primary space by perennial organisms in winter are mere consequences of earlier intense interactions.

WINTER COLONIZATION OF SETTLING BLOCKS

To determine whether the potential for colonization of free space existed during winter and thereby to provide a partial test of the second hypothesis, settling block experiments were conducted between November 1977 and February 1978. Settlement of significant numbers and variety of larvae on bare concrete blocks during this 3-month period would suggest that the potential for re-growth in winter was high, not restricted. Examination of 50 1-cm^2 quadrats on these settling blocks revealed very similar phyletic composition to that in the climax community blocks; juvenile *Spirorbis spirillum*, *Dendropoma lituella*, barnacles, and initial stages of 24 bryozoan colonies were found on the 3-month old settling plates. Unfortunately, small sizes of bryozoan ancestrula and their highly polymorphic morphology precluded our identifying them to species level. Combined densities of these juvenile organisms averaged $>2\ cm^{-2}$ and were frequently much higher. In addition, comparison of these data with the densities of newly settled larvae upon climax blocks revealed even higher densities on the latter, with average values on some blocks being 5 to 10 times greater. (An exemplary analysis of *Spirorbis* settlement is provided below.) It is clear that large numbers of larvae of numerous species were present during autumn and winter and that the clumped distribution of species on climax blocks cannot be simply explained away by an insufficiency of planktonic forms to settle on primary space.

PROCESSES INFLUENCING CLIMAX COMMUNITY STRUCTURE

Preferential settling among solitary species

A possible explanation for the failure of apparently abundant planktonic larvae to be found in open spaces on climax blocks (especially on Block 3 which was 85% open) is preferential settlement. Some substrata may confer higher survival value against physical and biotic pressure than others, and natural selection would be expected to favour some capacity for larval discrimination. Organisms with solitary

growth habits (compared with colonial forms) may be particularly vulnerable to both predation and overgrowth since there are physiological restrictions on maximal size that otherwise might confer a size refuge. Sufficient numbers of juvenile *Spirorbis spirillum* were available on our various types of community blocks to perform an analysis of the settling success of this solitary species on different blocks and substrata.

TABLE III

Density of juvenile and adult *Spirorbis* on treated and untreated blocks.

Block		Adult density No. individuals/cm^2	Juvenile density No. individuals/cm^2
1	$n = 50$	3.10	12.24
2	$n = 50$	0.74	4.88
3	$n = 50$	1.14	1.92
4	$n = 25$	2.08	1.64
	Untreatened half		
4	$n = 25$	–	0.96
5	Block with barnacles		
	$n = 25$	0	2.08
5	Half of scraped barnacle block		
	$n = 25$	–	8.12
6	3-month-old block		
	$n = 25$	0	1.82

Table III shows the densities of juvenile *Spirorbis* worms on each type of community block compared with adult densities. There were high densities of both juveniles and adults on Block 1 while juvenile densities were especially low on Block 3. Even with 100% survival of young on Block 3, *Spirorbis* would not have been so successful as on Block 1. Subsequent larval settling might potentially have increased the population of *Spirorbis* on Block 3, but its failure to evidence many juveniles when some neighbouring blocks were well colonized suggests restrictions of *Spirorbis* numbers. There appears to have been this same restriction on the 3-month old settling blocks as they supported the same low density of juveniles. This restriction, of course, may have been due to preferential settlement upon other substrata or to rapid selective mortality of larvae on exposed, open sites after indiscriminate settlement. The results in Table III show that the latter hypothesis is unlikely. All encrusting organisms (mainly barnacles) were thoroughly scraped off a fourth climax block in November 1977, producing a surface nearly indistinguishable from that on new blocks and open patches of climax Blocks 1 to 3. Only the faintest traces of barnacle bases were visible. Settling larvae should thus have been exposed to the same degree of predation, abrasion, etc. as larvae on other open spaces. Nevertheless, juvenile *Spirorbis* were 4 to 5 times as dense on this scraped surface as

on any other bare spaces. Furthermore, the number of tube remnants left by juvenile *Spirorbis* dying during the period was very low and equal on both scraped and new blocks. Interestingly, the unscraped half of the block cleared of encrusting forms contained only a very few juveniles or shell remnants. Apparently, larval *Spirorbis* simply did not settle here. It therefore seems that differential mortality of juveniles on bare surfaces is a very unlikely explanation for their low numbers on those climax community blocks with large proportions of free space. Preferential settlement on favoured substrata, which were not necessarily open primary space, seems more likely.

We examined in greater detail the types of substratum upon which juvenile *Spirorbis* had successfully settled during the autumn and winter. A single quadrat could contain up to seven different types of substrata (block or animal substrata), all in various relative densities. We, therefore, normalized *Spirorbis* densities across substrata by dividing juvenile numbers on a given substratum by the area occupied by that substratum type across all sampled quadrats on all blocks. Table IV in-

TABLE IV

The weighted density of juvenile *Spirorbis* on various substrata as compared with the percentage of adults occurring on each substratum: densities were weighted by dividing the number of individuals encountered on a particular substratum by the total area (cm^2) of that substratum available among all blocks.

Substratum	Weighted density of juvenile *Spirorbis* per cm^2	Adult occurrence (%)
Dendropoma lituella	19.65	2.4
Serpula vermicularis	18.72	1.7
Colletosia sp. D	18.00	–
Adult *Spirorbis*	13.33	6.0 (in 3D clusters)
Unidentified bryozoan sp. B	7.69	–
Schizoporella unicornis	5.66	–
Bare surface	4.69	82.6
Microporella sp. A	3.39	1.3
Barnacle bases	3.11	–
Microporella californica	1.86	–
Microporella sp. C	0.73	–
Hippodiplosia insculpta	0.60	0.7
Tubulipora sp.	0.50	1.7
Rhynchozoon tumulosum	0.53	3.3
Microporella ciliata	0.26	–
Barnacles	0.12	–

dicates that distinct differences in settlement patterns amongst substratum types were present in the climax communities. *Spirorbis* juvenile densities were highest on *Serpula vermicularis*, *Dendropoma lituella*, and adult *Spirorbis* (sometimes found in three dimensional clusters), as well as on the bryozoan *Colletosia* sp. Open primary space is found well down on the list. Correlatively, the highest proportions of *Serpula*

vermicularis, *Dendropoma lituella*, and adult *Spirorbis* occurred on Block 1 on which free space was minimal (Fig. 1). It seems that certain living substrata proved more attractive to larvae, and community blocks with these substrata accumulated *Spirorbis* juveniles. Unfortunately, other species were either too rare or too small as juveniles for similar analyses to be conducted so we cannot evaluate the importance of differential settlement by these organisms.

Overgrowth by colonial species

In contrast to solitary species which have little capacity to competitively dominate other organisms, colonial organisms, typified by bryozoans, frequently grow over many other species, resulting in the gradual death of the overgrown organisms. Thus, in communities in which nearly all organisms tend to be closely associated in space, overgrowth is another potentially important structuring mechanism that may help to explain patterns in the climax community blocks. We examined the number of different substrata (mainly living animals) upon which each bryozoan was found growing to evaluate whether a capacity for overgrowth correlated with numerical predominance in the community.

Table V summarizes the results of this examination. As expected, the most abundant bryozoan species tended to be found on the largest number of substrata. The two most common species were found on five substrata, three of which were other bryozoans, while less common species tended to be on fewer substrata. Rare species generally covered $<2\%$ of the total area occupied and yet comprised a third of all bryozoans. In contrast to more common species which frequently overgrew other organisms, rare species almost exclusively utilized small gaps of open primary space between larger colonies of common species. Rareness was thus associated with the lowest observed incidence of overgrowth, while numerically predominant species showed the highest capacity for overgrowth (and were not abundant merely because of a single widely distributed type of substratum). On the other hand, it is also striking that each bryozoan was apparently very limited in the numbers and types of species which it overgrew. Of the 27 possible species that could have been overgrown, no bryozoan species was found in our samples to be overlying more than four other species. Most overgrew only one or two others. The five most common bryozoans in Table V together covered nearly two thirds of the area of the substratum occupied but less than one third of the species on the climax blocks. Overgrowth, although widespread, was apparently very selective in this community.

A plexus diagram (Fig. 2) summarizes the overgrowth relationships among both colonial and solitary species observed in our samples from the climax blocks. A low incidence of overgrowth among most species is clear from the figure, but few species were unconnected to at least one other. The five species in the centre of the figure displayed the largest number of connections with other species and were also among the most abundant organisms on the blocks. Nevertheless, within this group,

abundance and number of connections were not correlated: the most abundant bryozoan *Rhychozoon tumulosum* associated with only half the number of species that *Hippodiplosia insculpta* or *Tubulipora* sp. had contacted. As a group the highest frequencies of overgrowth (i.e., for any particular species, the fraction of all observations in which there was overgrowth) involved these five common species but more than half the interactions were as substrata upon which others were growing. In fact, nearly every species in the climax communities had managed to overgrow these common and supposedly dominant species at least once in our sampled

TABLE V

Characterization of substrata occupied and area covered by bryozoans on climax community blocks: maximum possible coverage is 50 cm^2.

Bryozoan species	Total area (cm^2)	Observed substratum	Number of substrata
Rhynchozoon tumulosum	11.05	Bare substratum, *Spirorbis*, 3 spp. bryozoan	5
Hippodiplosia insculpta	7.46	Bare substratum, *Spirorbis*, 3 spp. bryozoan	5
Tubulipora sp.	7.08	Bare substratum, *Spirorbis*, *Serpula vermicularis*, 1 sp. bryozoan	4
Microporella sp. C	5.44	Bare substratum	1
Microporella sp. A	5.03	Bare substratum, *Serpula vermicularis*, 1 sp. bryozoan	3
Microporella ciliata	3.85	Bare substratum, 2 spp. bryozoan	3
Microporella californica	2.62	Bare substratum, *Spirorbis* 1 sp. bryozoan	3
Smittina landsborovii	2.36	Bare substratum, 1 sp. bryozoan	2
Callopora horrida	2.21	Bare substratum, *Spirorbis*, 1 sp. bryozoan	3
Unidentified bryozoan sp. B	1.68	Bare substratum, 1 sp. bryozoan	2
Microporella sp. E	1.03	Bare substratum, *Spirorbis*	2
Unidentified sp. B	1.05	Bare substratum	1
Fenestrulina malusi	0.93	Bare substratum, *Spirorbis*	2
Hincksina velata	0.82	Bare substratum, *Spirorbis*, 2 spp. bryozoan	4
Schizoporella unicornis	0.53	Bare substratum, 2 spp. bryozoan	3
Unidentified bryozoan sp. D	0.58	Bare substratum	1
Hippothoa hyalina	0.60	Bare substratum	1
Dendrobeania lichenoides	0.35	Bare substratum	1
Colletosia sp.	0.46	Bare substratum, *Spirorbis*	2
Bugula pacifica	0.28	Bare substratum	1
Chapperia patula	0.09	Bare substratum	1
Beania sp.	0.01	Bare substratum	1

quadrats. Certain rarer species (e.g., *Hincksina velata*, *Balanus glandula*) even seemed to overgrow selectively one or more of the most common species, while not overgrowing the less common forms. Hence, predominance on a given block did not necessarily imply suppression of the less common forms.

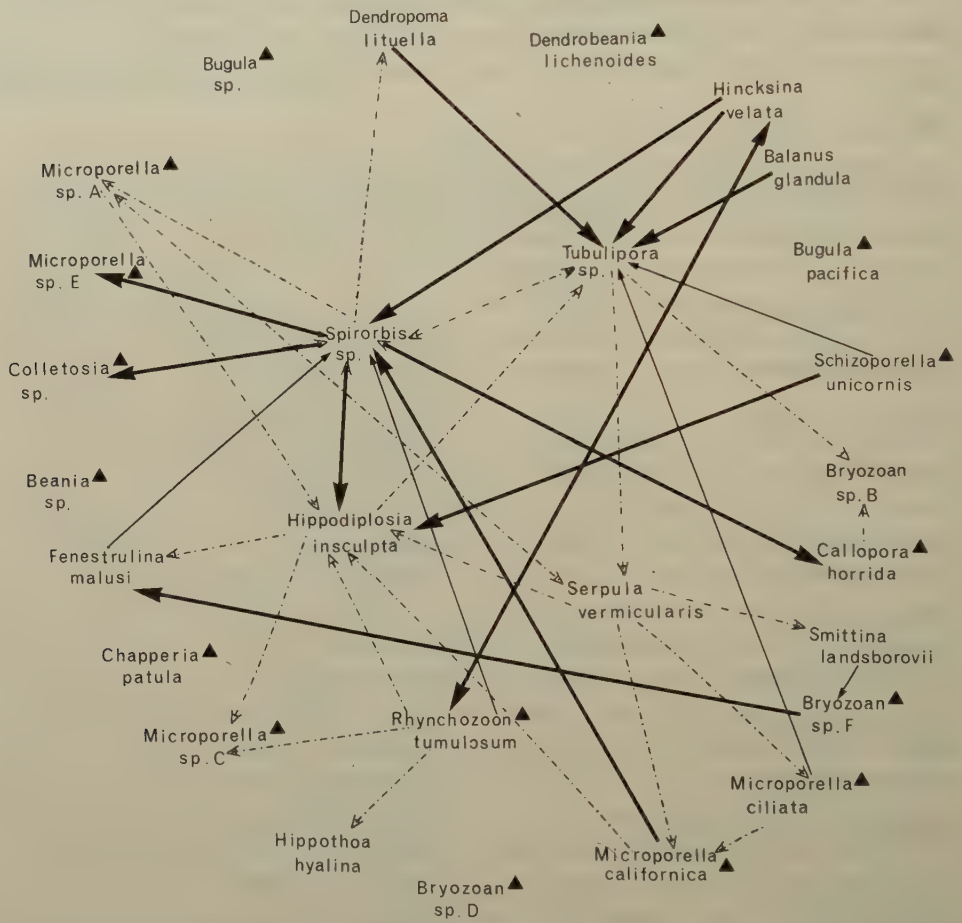

Fig. 2. Plexus diagram showing the overgrowth patterns observed in the climax communities: arrows indicate the direction of overgrowth and the thickness of the arrow indicates the frequency of the observed overgrowth: the presence of a morphological defence is also shown for bryozoan species; 11 to 33% occurrence ⟶; 5 to 10% occurrence ⟶; 1 to 5% occurrence -·-·-·-⟩; ▲, Bryozoa with morphological defence.

Finally, the large number of interactions between solitary forms like *Spirorbis* worms and colonial bryozoans does not necessarily imply mortality to the overgrown organism. Because of its small coverage, overgrowing *Spirorbis* rarely seemed to have any negative impact on the spreading bryozoans. Likewise, bryozoan over-

growth of *Spirorbis* seldom seemed to kill the worm. Completely overgrown worm tubes often remained open at the aperture and the apertures protruded above the bryozoan colonies.

Discussion

To study climax patterns of encrusting community organization on the bottom surfaces of natural boulders, easily sampled mimics of rocks in the form of 900-cm^2 flat concrete blocks were employed. Species composition of both natural and artificial boulders was typical of north-temperate Pacific intertidal communities (Kozloff, 1974; Smith & Carlton, 1975), and we assume that similar rules of organization apply to each. Data from Osman (1978) suggest that both the size and exposure times of our blocks were sufficient to produce climax communities. First, Osman found that rocks 500 to 1000 cm^2 in surface area were very infrequently disturbed by water action; our 900-cm^2 blocks were also sufficiently well sheltered against wave and current action that disturbance was very unlikely. There was no evidence of any broken remnants, attachment bases or other signs of mechanical disruption even though exposed beaches experienced the heaviest storms in 25 yr immediately before sampling. Secondly, in studying benthic epifauna, Osman (1978) found that species number and composition on replicate plates exposed during autumn, winter or spring converged and stabilized at the end of the following summer. Plates exposed in summer converged by early in the next summer. Similar, stable communities were thus present within 1 yr on all plates. Because our blocks were exposed for 3.3 yr, it is very likely that stable, self-replacing (climax) assemblages of organisms were present when sampled in the winter 1977–78. Thus, rare species, like common ones, are assumed to have been at equilibrium densities and not the result of only recent immigration.

Climax blocks were characterized by a surprisingly large and variable quantity of free primary space that lacked any evidence (e.g., base remnants) of previous occupation by encrusting forms. Species normally abundant only in summer had probably occupied much of this space and abandoned it in early autumn. Curiously, neither planktonic larvae, which proved to be relatively abundant even during winter conditions, nor spreading adult colonies seemed to expand appreciably into this vacated space. Settlement of larvae such as *Spirorbis*, although less frequent than during summer, was relatively heavy on and adjacent to other organisms but less common in these patches of open bare space. Similarly, despite available primary substratum, colonies of bryozoans commonly overgrew others. Contrary to our expectations, we could find no relationship between the frequency of secondary space settlement (on other individuals) or colonial overgrowth and the availability of primary space. Likewise, species diversity was unrelated to available space. Instead organisms tended to be clumped, situated on or adjacent to each other on small areas of

primary substratum, independent of their size or the total amount of free space of the block. Large patches of open primary substratum were apparently less relevant to the diversity and distribution of these perennial encrusting organisms than the distribution and abundance of organisms already resident.

The selection pressures favouring encrusting organisms that clump, overgrow and settle on each other may be related to probable heavy occupation of primary space by seasonally (summer) abundant species. It is well known that sponges and colonial tunicates, for example, can have devastating effects on bryozoans near their bases. Gordon (1972) states that even short-lived sponges leave a weft of spicules on the substratum that prevents bryozoan growth. Similar effects may be expected for solitary animals like *Spirorbis*. We found only a few remnants of spicules on our blocks, but earlier survey work during the summer 1977, at nearby Sepping's Island (1 km from our study site on Diana Island) showed up to 85% space occupation, much of it by sponges and colonial tunicates. Seasonal shortages of primary space produced through colonization by these kinds of superior competitors may select for perennial understory species that avoid interactions with dominants and instead have abilities to exploit each other as substrata.

There are several potential advantages to overgrowth and secondary space settlement that may partially compensate for the costs of competition with earlier encrusting occupants. First, if the likelihood of outcompeting a current occupant is high, it may pay invaders to seek these species out and selectively settle. The presence of certain other organisms may also indicate that this portion of the habitat is suitable for survival. In addition, there may be physiological advantages to growing on a particular biotic substratum rather than an abiotic one. For example, Hunt (1970) suggests that sulphated mucopolysaccharides used in the calcification of bryozoans and other animals may result from trapping molluscan mantle mucin secretions to bond the colonizer to its animal substratum. In such cases, the resulting resistance to disturbance would be a distinct advantage to settlement or overgrowth onto specific calcareous surfaces.

Larval settlement in *Spirorbis* during the winter indicated that larval densities varied greatly from block to block within the climax community. These differences seem best explained by preferential settlement (a form of overgrowth) on the tubes of *Dendropoma lituella*, *Serpula vermicularis*, adult *Spirorbis*, and several species of bryozoans. Blocks with the largest proportions of these animals (all with calcareous surfaces) attracted the highest members of juvenile *Spirorbis*.

Analysis of the close associations between these encrusting animals reveals several processes that influence the patterns of diversity and spatial arrangement observed. At a macroscopic level, each block contained only a limited selection of the 27 species found, 3 or 4 solitary species and 9, 10 or 14 bryozoan species. Despite the close proximity of the blocks (a few metres) the particular species of colonial bryozoans differed strongly among the blocks, with only two species common to all and just six species resident on two blocks. In some sense, there appear to be several possible

climax states which seem to be structurally similar but which differ in the presence of particular species and in their relative coverages. Sutherland (1974) proposed the existence of alternative stable assemblages in benthic communities. He argued that certain species can impart some degree of stability to the assemblage by resisting larval invasion of certain other species (Sutherland, 1977). Presumably active choice of settlement location by larvae should achieve the same result. Sutherland thus argues that while the occupation of free space is dependent upon the number and type of larvae available, the fate of secondary space depends to a large extent on the identity of the species currently occupying that space. This argument should be particularly true when overgrowth by each species is also limited to only certain species. Such "priority effects", detailed by Sutherland (1978) for the bryozoan *Schizoporella* and the tunicate *Styela*, may have produced on our blocks apparently alternative "stable" assemblages in which differences in early colonization resulted in subsequent exclusion of a sizable fraction of the potential colonists. At "climax", minimally overlapping groups of compatible species seemed to exist on different blocks.

Unfortunately, the mechanisms by which species can be excluded by other species are not clear. Mechanical defences may be involved in some cases, but few of the common species on our blocks were defended in this way. Both endocrine or ectocrine release (Knight-Jones & Moyse, 1961) and toxin secretion (Jackson & Buss, 1975) have been suggested as possible defences against settlers. Conversely, settling larvae or adjacent colonies may be able to detect chemical or textural information leading to avoidance of certain substrata.

In contrast to interblock exclusiveness, intrablock compatibility of species seemed to preclude any single species from monopolizing resources. We observed obvious mortality among certain species caused by overgrowth of other species, but frequent reversals of the interaction were also seen. Thus, many species seemed to overgrow and be overgrown with about the same frequency. In general, the common bryozoans on each block displayed no mechanical defenses and were regularly overgrown by four to eight other species (Fig. 2). Nevertheless, they were able to thrive in this situation because they were also able to overgrow several of these same competitors, plus one or two other species as well. Less common species almost always overgrew at least one other species, but often the latter could not in turn overgrow the former. A group of one-way overgrowth relationships existed among less common species on each block in which no single species was spared. The rarest species in contrast were seldom seen overgrowing other species, but neither were they often observed being overgrown. Interestingly, the six unconnected rare species in Fig. 2 all have good mechanical defences. In short, those species able to be overgrown were found with equal frequency overgrowing at least one other species (Fig. 2). Jackson (1977) described a similar situation as a competitive network in which each species has a series of competitive connections, predictably losing some interactions but winning others. No species, however, is ever able to dominate all others and a continuously

changing mosaic of species, perhaps in a cyclical fashion, occurs at "equilibrium".

Rhynchozoon tumulosum is the only common species that did not seem to follow this pattern. Its behaviour seems more like that of well defended rare species. Unlike the other common bryozoans, it has good mechanical defences and only two other species were observed overgrowing it. Similarly, it only infrequently overgrew other species and only three species were ever observed threatened by *Rhynchozoon*. For some unknown reason it was able to colonize (mainly bare space) in all three communities whereas others of its type were restricted to only one block.

The structure and spatial relationships of this intertidal encrusting community can be summarized as follows: on a gross scale, seasonally abundant forms probably outcompeted most encrusting species and thereby produced sizable patches of bare space in autumn. Nevertheless, few larvae settled on and few colonies spread into this space, but instead accumulated in taxonomically restricted aggregations ("communities") of mutually overgrowing species. The compositional distinctness of these alternative aggregations suggest active defences which could be overcome by only a limited number of species. Within these aggregations a continuous scramble among near equals seems to produce a temporally dynamic mosaic.

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OXYGEN CONSUMPTION AND THE OCCURRENCE OF A HAEMOPROTEIN WITHIN THE CENTRAL NERVOUS TISSUE OF THE HOPLONEMERTEAN *AMPHIPORUS LACTIFLOREUS* (Johnston) (NEMERTEA : ENOPLA : MONOSTILIFERA)

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Abstract: The red pigment occurring intracellularly within the cerebral ganglia and lateral nerve cords of *Amphiporus lactifloreus* (Johnston) has been investigated by histochemical, cytochemical, and microdensitometric means. A non-enzymic peroxidase activity distributed homogeneously throughout the cytoplasm of certain glial cells is demonstrated. Specific histochemical results and characteristic absorption spectra confirm that the pigment is a haemoprotein. Rapid de-oxygenation and subsequent re-oxygenation of the pigment in conditions of fluctuating oxygen tension indicates that the haemoprotein is physiologically active.

Respiratory data have been obtained for *A. lactifloreus* and these are compared with the results published for the freshwater nemertean *Prostoma graecense* (Bohmig). Carbon monoxide interferes with the neuro-pigment and treatment with this gas results in a 50% reduction in respiratory rate and oxygen consumption. Graphs of oxygen consumption and body weight, both on a $\log_{10}$ basis, are depicted and discussed.

The possible rôle of the pigment in facilitative diffusion of oxygen within the nemertean central nervous system is discussed.

INTRODUCTION

The intimate association between haemoglobin and certain elements of the nervous system was first recorded by Lankester (1872) after a microspectroscopic examination of the nerve cord of the marine polychaete *Aphrodite aculeata*. Intracellular haemoglobins have since been reported from the central nervous tissues of many representatives of several invertebrate phyla (Wittenberg *et al.*, 1965; Prosser, 1973a; Weber, 1978), including the Nemertea (Hubrecht, 1875; Wittenberg *et al.*, 1965; Vernet, 1973).

Of the commonly occurring littoral nemertean species found around the British Isles, several have been observed to possess a red pigment in association with their nervous systems. These include *Amphiporus lactifloreus* (Johnston), *Lineus ruber* (O. F. Müller), *L. longissimus* (Gunnerus), and *Emplectonema gracile* (Johnston). Little published research, however, has been specifically concerned with nemertean neuro-pigments. Wittenberg *et al.* (1965) and Vernet (1973) suggested that the red neuro-pigments in *Amphiporus* sp. and in three species of the heteronemertean genus *Lineus*, respectively, were haemoglobin. Their conclusions were based mainly on the

observation that the pigments exhibited remarkably similar absorption spectra to those obtained from vertebrate corpuscular haemoglobin. Keilin & Hartree (1951) suggested, however, that the classification of biologically active compounds, such as oxygen carriers, should be based not upon their physico-chemical properties but upon their specific biological activities and the nature of their prosthetic groups. In this way they were able to unite all protohaem–protein oxygen-carriers into a single group – haemoglobin. As no information has been published to date on the function or mode of action of the nemertean neuro-pigments, it would appear injudicious to refer to this "... diffused colouring matter ..." (Hubrecht, 1875, p. 254) as haemoglobin sensu stricto.

Relying upon non-specific histochemical tests, Poluhowich (1970) concluded that the red pigment present in the blood system of the freshwater hoplonemertean *Prostoma rubrum* (Leidy) [= *P. graecense* (Bohmig)][1] was haemoglobin. In the same paper he published respiratory data for this species and further concluded that the pigment allowed the worms to respire at a constant rate under conditions of low environmental oxygen tension. He did not, however, attempt to postulate a specific mode of action for the pigment.

It has been suggested that intracellular respiratory pigments serve one, or a combination of several, possible functions. These include various catalytic functions within the cell, the storage of oxygen to prevent local anoxia, and to facilitate the entry of oxygen into tissues (Kreuzer, 1970; Wittenberg *et al.*, 1975). Accordingly, the vast majority of experimental work in this area has been directed towards the elucidation of myoglobin function in vertebrate skeletal muscle (Wittenberg *et al.*, 1975). The functions of invertebrate intracellular respiratory pigments are, not surprisingly, incompletely understood. It is, however, interesting that Wittenberg (1970) and Weber (1978) have shown the intracellular haem-globin complexes found in many invertebrates to be monomeric, with molecular weights approximating to those of vertebrate myoglobins (17000d).

Schindelmeiser *et al.* (1979) reported the presence of haemoproteins in the glial cells of the freshwater molluscs *Lymnaea stagnalis* and *Planorbarius corneus*. As normal nervous function is based upon the intimate interactions between neurons and glial cells they suggested that the glial cells served to increase the respiratory area of the neurons in order to ensure adequate diffusion of respiratory gases. In the present investigations the red pigment impregnating certain glial cells (Bullock & Horridge, 1965) of the cerebral ganglia and lateral nerve cords of the hoplonemertean *Amphiporus lactifloreus* has been examined histochemically, cytochemically, and densitometrically. The intimate relationship between the glial cells and the rest of the central nervous tissue which, "... does not seem to have been very thoroughly investigated, ..." (Willmer, 1970, p. 275) has been examined in more detail in the light

[1] Gibson & Moore (1976) invalidated the species *Prostoma rubrum* and concluded that the nemertean species examined by Poluhowich (1970) was *P. graecense*. The present paper conforms with Gibson and Moore's re-classification.

of the present findings. Data on oxygen consumption and respiratory rates have also been obtained in order to compare these values with those of *Prostoma graecense* (Poluhowich, 1970). Finally, suggestions have been made for the physiological rôle of the nemertean neuro-pigment.

Materials and Methods

Animals used for the study were collected from coarse sand and shell gravel found beneath rocks lying within the mid-littoral zone of the beach at Trwyn-y-Penrhyn, Anglesey, N. Wales. They were kept alive in glass troughs containing ≈3 l of continuously aerated sea water at 8–13 °C. Small numbers of the amphipod crustacean *Gammarus locusta* (L.) were provided ad libitum, as these have been shown to be readily taken by captive *Amphiporus lactifloreus* (Jennings & Gibson, 1969).

The distribution of non-enzymic peroxidatic activity in whole mounts fixed in 10% formalin in 0.1 M sodium phosphate buffer, pH 7.0, at 1–5 °C was studied with the cyanol blue technique (Dunn, 1946), a benzidine-hydrogen peroxide method (Knox, 1954), and a method utilizing 3,3′-diaminobenzidine tetrahydrochloride (DAB; from Sigma London Chemical Co. Ltd.), modified from Goldfisher (1967), employing a final substrate concentration of 0.02% hydrogen peroxide (Venkatachalam *et al.*, 1970). In addition, the latter technique was applied to 10-μm cryostat sections cut from tissue fixed as above for varying periods up to 1 month. Incubation periods of up to 30 min, at room temperature, were employed and the standard controls for discrimination between true and non-enzymic peroxidases were routinely applied (Venkatachalam *et al.*, 1970; Phillips, 1978).

The procedure followed for the cytochemical localization of non-enzymic peroxidatic activity was modified from that of Phillips (1978). In the present study the cephalic portions of decapitated *A. lactifloreus*, containing the cerebral ganglia, were substituted for *Paravortex*. Semi-thin sections, 0.5–1.0 μm in thickness, were cut from the resin blocks. These were either stained with 0.5% Azure II in 1% aqueous sodium tetraborate or left unstained and viewed by conventional light microscopy. Tests, permitting discrimination between various forms of non-enzymic peroxidases, were applied as described by Roels *et al.* (1975), Fahimi (1979), and Litwin (1979).

Absorption spectra of the pigment were obtained using a Vickers M86 Microdensitometer operating in the visible range. Preliminary experiments showed that the pigment impregnating the cerebral ganglia of decapitated worms, previously narcotized in a 2% solution of propylene phenoxetol in sea water, gave spectral curves directly comparable with those obtained from the pigment of small, intact, non-narcotized individuals. The results obtained from these experiments were also directly comparable with those attributed, by other authors, to represent the oxy-

genated state of haemoglobin (Lee & Smith, 1965; Prosser, 1973a; Vernet, 1973). The worms were, therefore, narcotized and decapitated immediately prior to mounting on glass slides and viewing in the Microdensitometer. A shift in spectral maxima towards a result directly comparable with that of de-oxygenated vertebrate haemoglobin (Prosser, 1973a) was induced by the application of a coverslip to the above preparation.

In order to determine what effect carbon monoxide would have on the spectral properties of the red pigment the purified gas was bubbled, at a rate of 20 ml gas · 100 ml sea water^{-1} · min^{-1}, through the sea water containing the worms. This was continued for at least 4 h prior to analysis of the pigment.

Preliminary experiments to determine the effect of exposure to carbon monoxide on oxygen uptake were performed using an oxygen electrode (polarographic) technique to be described in more detail elsewhere (Varndell, in prep.). Briefly, live worms were weighed and then placed in a chamber containing a known volume of sea water through which carbon monoxide and air, other gas mixtures, or air alone had been bubbled for 4 h prior to the start of the experiment. Samples of the water were removed at frequent intervals and subjected to a modified Winkler technique to determine dissolved oxygen concentration. These values were then checked against those obtained polarographically. The experimental chamber was sealed for 10 min after which time a small volume (0.1 ml) was removed. An oxygen-loss determination was performed against a control (i.e., without worms) using a Radiometer (Copenhagen) E5046 P_{O_2} electrode enclosed within a temperature-regulated cell at 14 °C. A polarizing voltage of 630 mV was applied to the cathode and the current generated, proportional to the amount of oxygen in solution, was measured on a calibrated scale. The chamber was carefully flushed with clean sea water and three determinations for each worm were obtained. Finally, the dry weight of each worm was measured after drying to constant weight in pre-weighed aluminium containers at 95 °C.

Modifications to the method for the determination of oxygen tensions, as suggested by Oeseburg *et al.* (1979), for example decreasing the polarizing voltage and substituting different electrode buffers, were tested but not routinely employed.

Results

Most haemoproteins exhibit a non-enzymic peroxidatic activity due to the presence of a metalloporphyrin prosthetic group in their structure (Essner, 1974). Typically this activity, which requires the presence of hydrogen peroxide as substrate, is heat-stable and relatively cyanide insensitive. It is also evident even after prolonged aldehyde fixation (Essner, 1974). Such an activity (Table I) is shown by certain (glial) cells in the cerebral ganglia and lateral nerve cords of *Amphiporus lactifloreus* following application of the DAB technique (Fig. 1). Fig. 2 shows that some of these

TABLE I

The degree of staining under certain conditions with DAB on the cerebral ganglia of *Amphiporus lactifloreus*: 2 mg DAB/ml at 20 °C for 30 min on 10-μm cryostat serial sections, prefixed for 24 h in 10% neutral buffered formalin (see text) except where stated otherwise: increase in density represented by increase in + → + + + +.

Final substrate concentration (%)	Special conditions	Relative density of final reaction product
0.02	None	+ + + +
Zero	None	–
2.00	None	+
0.02	Formalin fixation, 2 h–4 wk duration	+ + + +
0.02	Heat (95 °C for 60 min)	+ + +
0.02	KCN 5×10^{-2} M	
0.02	KCN 5×10^{-3} M	+ +
0.02	KCN 5×10^{-4} M	+ + + +

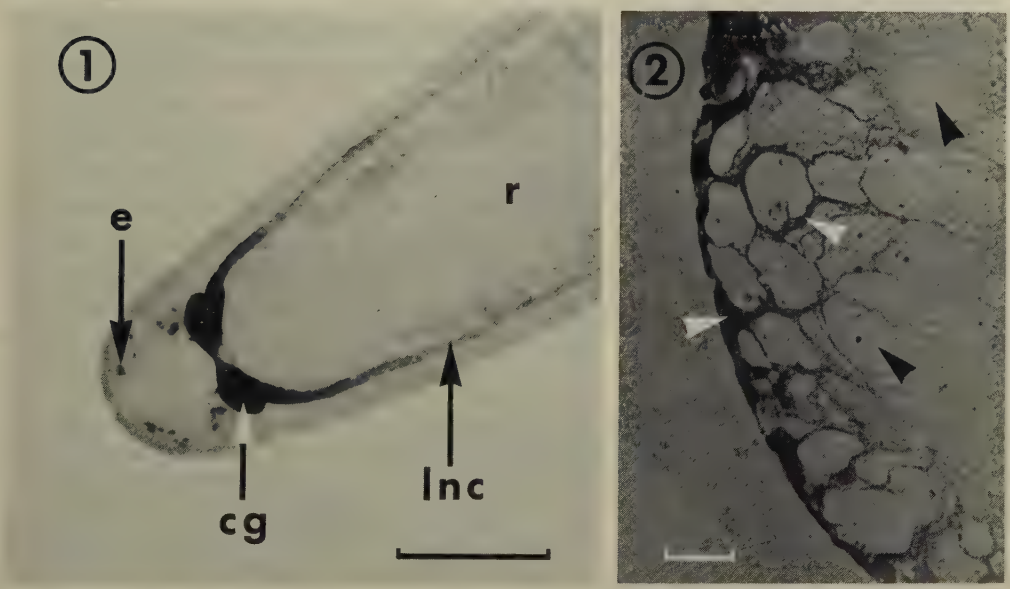

Fig. 1. Distribution of non-enzymic peroxidase activity in the cerebral ganglia (cg) and lateral nerve cords (lnc) of *A. lactifloreus* as shown by the localization of oxidized-DAB reaction product: e, eyes; r, rhynchocoel; scale bar = 1 mm.

Fig. 2. Semi-thin (1 μm) section showing oxidized-DAB reaction product (white arrows) in a layer of specialized glial cells round the unipolar nerve cells (black arrows) in the cerebral ganglia of *A. lactifloreus*; scale bar = 10 μm.

non-nervous supportive cells lie immediately beneath the outer connective tissue sheath, forming a squamous monolayer peripheral to the mass of unipolar nerve cells and their associated neuropil. Although distinct, due to the density of the oxidized-DAB reaction product within the glial cells, their morphology is uncertain; they appear, however, to surround all the neuronal somata and axons of the cerebral ganglia and lateral nerve cords. Bullock & Horridge (1965, p. 583) reported that prominent glial cells occurred "... especially in the fibrous core"; however, no evidence has been obtained to suggest that there are non-enzymic peroxidases in these cells. Likewise, no localization of a reaction product has been observed in the peripheral nerves of the body wall or in the 14 longitudinal proboscidial nerves (Fig. 1), even when the proboscis was incubated alone in the DAB medium. The cell bodies of these nerves are, however, located within the central nervous tissue and it is conceivable that these somata are served by glial cells containing neuro-pigments. Preliminary electron microscopic observations have revealed that the reaction product of the DAB technique occurs homogeneously throughout the cytoplasm of the stained cells. A similar finding was reported by Phillips (1978) in the cells surrounding the extrinsic pharyngeal musculature of the entosymbiotic rhabdocoel *Paravortex scrobiculariae*. Houk & Beck (1976) also reported a non-localized distribution of

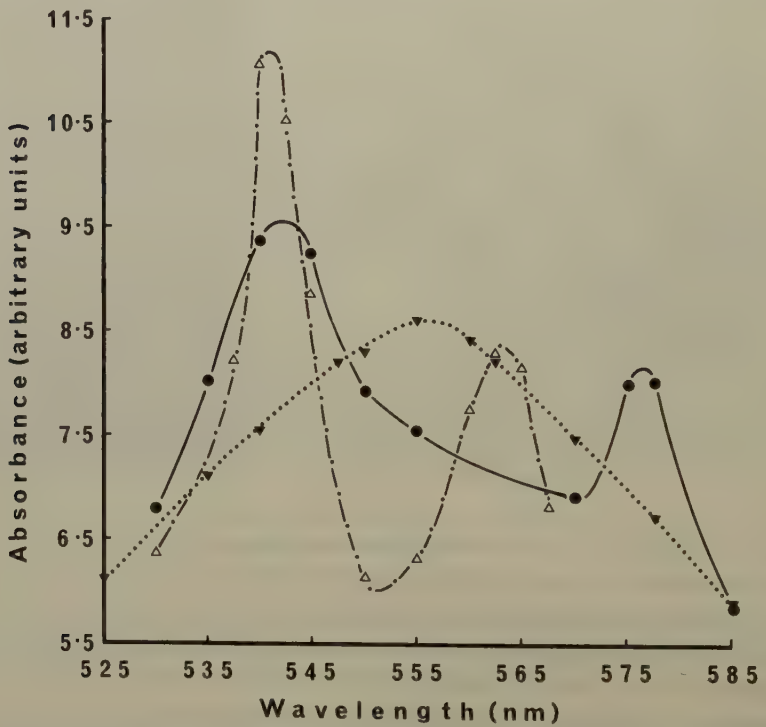

Fig. 3. Absorption spectra obtained for the red neuro-pigment of *A. lactifloreus*: ●, presence of oxygen; ▼, anaerobic conditions; △, presence of carbon monoxide.

oxidized-DAB reaction product within the glial cells of the corn borer *Ostrinia nubilalis*. In this case, however, the oxidation of DAB occurred in the absence of exogenous hydrogen peroxide substrate and was attributed by Houk & Beck (1976) to be due to an amine oxidase (monoamine: O_2 oxido-reductase (deaminating) E.C. 1.4.3.4).

Absorption spectra characteristic for the red neuro-pigment within the yellow-green visible region are depicted in Fig. 3. Mean wavelengths, with 95% confidence limits for each peak, have been calculated from 15 individuals and the results are as follows: (i) presence of oxygen, 576.8 ± 0.4 nm (α) and 542.3 ± 0.3 nm (β); (ii) absence of oxygen, 555.8 ± 0.3 nm; (iii) presence of carbon monoxide, 562.6 ± 0.4 nm (α) and 541.2 ± 0.4 nm (β).

In comparison with the present results Wittenberg *et al.* (1965) recorded oxyhaemoglobin peaks at 578 nm and 540 nm, and similar values were reported by Vernet (1973) at 580 nm and 540 nm in situ and 544 nm in vitro. It is interesting that the β-band absorption intensity (Fig. 3) is greater than that in the α-band whereas normally the reverse is the case. This feature has been observed in the nematodes *Ascaris lumbricoides* and *Strongylus* sp. (Lee & Smith, 1965) and at least in these two species the haemoglobins involved have very high oxygen affinities.

The application of a coverslip to the mounted specimens caused an almost instantaneous shift in absorption spectra. In all the cases observed the double peak, a characteristic of the pigment when in the presence of oxygen, was replaced by a single peak within three minutes of the denial of air. A comparable rapid fading of the oxyhaemoglobin bands in anaerobic conditions was observed by Wittenberg *et al.* (1965). Re-establishment of the double peak was occasionally observed after removal of the coverslip but this was a much slower process and often required

TABLE II

Respiratory data for control and carbon monoxide treated groups of two species of nemertean: a, temperature = 14 ± 0.5 °C, 5.88 ml $O_2 \cdot l^{-1}$ sea water; b, figures from Poluhowich (1970), temperature = 20 °C; c, 95% confidence limits for $n = 50$; d, limits of accuracy not defined by Poluhowich (1970), $n = 49$.

Respiratory data	Species		
	Amphiporus lactifloreus[a]		*Prostoma rubrum*[b]
	Control	CO-test	Control
Oxygen consumption (range) ($\mu l\ O_2 \cdot worm^{-1} \cdot h^{-1}$)	0.11–3.62	0.08–1.94	0.012–0.840
Oxygen consumption (mean) ($\mu l\ O_2 \cdot worm^{-1} \cdot h^{-1}$)	1.75	0.93	–
Dry weight (range) (mg)	0.78–11.81	1.34–10.69	0.038–0.399
Respiratory rate (mean) ($\mu l\ O_2 \cdot mg\ dry\ wt^{-1} \cdot h^{-1}$)	0.334 ± 0.028[c]	0.174 ± 0.020[c]	0.700 ± 0.071[d]

several minutes for completion. The degree to which the physiological state of the preparation affects this re-establishment, however, is not known. *Amphiporus lactifloreus* kept under nitrogen for 48 h all showed absorption spectra characteristic of those exhibited in the presence of oxygen. It is likely, therefore, that there is rapid re-oxygenation of the pigment when the physiological state of the worm is good. Worms subjected to the continual bubbling of carbon monoxide through the sea water in which they were living survived, at room temperature, as long as the control worms. This experiment was terminated after 5 days with a 20% mortality.

Table II shows the respiratory data obtained from two groups of *A. lactifloreus*, each containing 50 individuals. The groups were: (i) control – subjected to aerated sea water alone, and (ii) CO-test – subjected to aerated sea water through which carbon monoxide had also been bubbled for 4 h immediately prior to the start of the experiments. A test of significance applied to the difference between the two respiratory rate means for *A. lactifloreus* gives $P < 0.001$. This indicates that treatment of *A. lactifloreus* with carbon monoxide has a profound effect on respiration rate which decreases markedly. Poluhowich (1970) observed a similar decrease under the same conditions for the freshwater *Prostoma graecense*, the control results of which are included in Table II.

TABLE III

Respiratory data for two groups of *Amphiporus lactifloreus* at 14 ± 0.5 °C under low oxygen tensions: a, 95% confidence limits for $n = 10$.

Respiratory data	Environmental oxygen tensions	
	15.5 mm Hg	1.75 mm Hg
Oxygen consumption (range) ($\mu l\ O_2 \cdot worm^{-1} \cdot h^{-1}$)	0.44–2.46	0.66–2.52
Oxygen consumption (mean) ($\mu l\ O_2 \cdot worm^{-1} \cdot h^{-1}$)	1.22	1.42
Dry weight (range) (mg)	1.88–5.78	1.88–9.40
Respiratory rate (mean) ($\mu l\ O_2 \cdot mg\ dry\ wt^{-1} \cdot h^{-1}$)	0.340 ± 0.064^a	0.332 ± 0.063^a

Table III shows the respiratory data obtained from two further groups of *Amphiporus lactifloreus*, each containing 10 individuals. Air–nitrogen mixtures were used in these experiments with final oxygen tensions of 15.5 mm Hg (10% standard air–oxygen level) and 1.75 mm Hg ($\approx 1.1\%$ standard air–oxygen level). There is no statistically significant difference between either of the mean respiratory rates given in Table III with that of the *A. lactifloreus* control group in Table II.

In order to compare more closely the respiratory rates obtained from different animals it is necessary to plot the oxygen consumption per worm against fresh

(live) body weight on a double logarithmic graph. Fig. 4 depicts such a graph for *A. lactifloreus*. The allometric equation $Y = aX^b$ equates oxygen consumption (Y) with a fractional power function of the animal's weight (X^b) (Zeuthen, 1953). Exponent b is the ratio of the percentage change in Y to the corresponding change in X and its value normally lies between 0.67 and 1.00, never exceeding the latter figure.

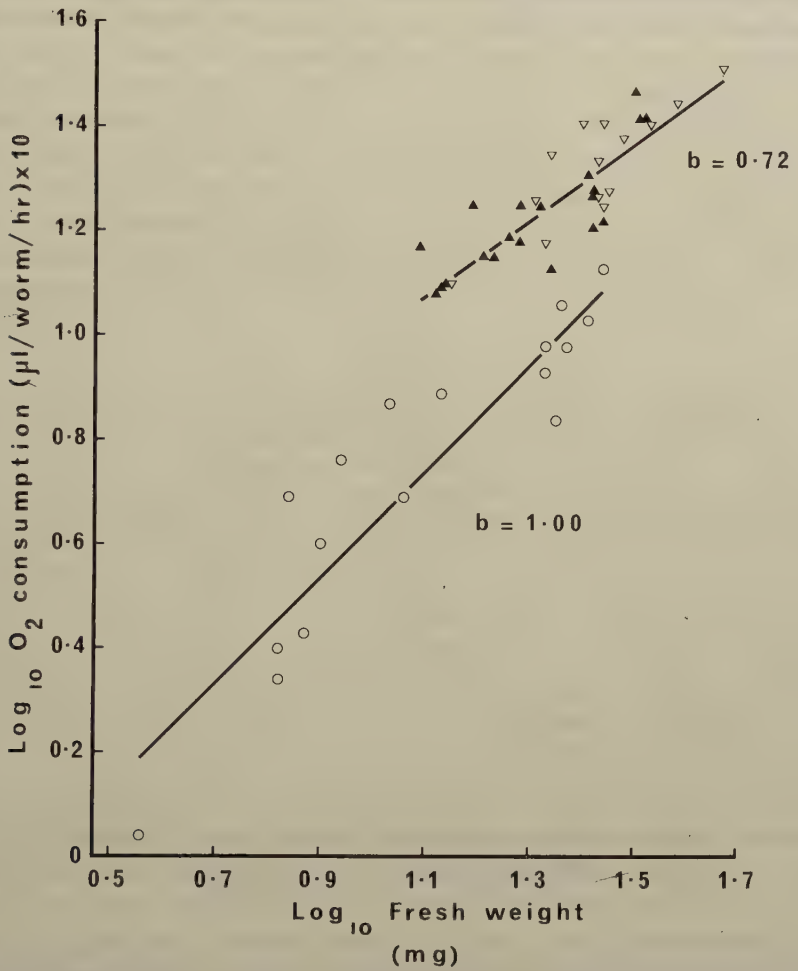

Fig. 4. Double logarithmic$_{10}$ plot of oxygen consumption as a function of body weight: the curves were calculated by linear regression analysis; control group of animals ($n = 50$); ▽, mature females; ▲, mature males; ○, immature worms.

In the case of *A. lactifloreus* two distinct linear regression curves can be drawn through the points displayed. One, with $b = 0.72$ and coefficient of determination (r^2) = 0.75, was calculated for all the specimens observed with mature gonads. The other, $b = 1.00$; $r^2 = 0.85$, was calculated for the immature specimens. Zeuthen (1953) predicted

a *b*-value of 0.95 for animals below ≈40 mg live body weight. His prediction did not, however, account for varying oxygen requirements during development. It is reasonable to suggest, therefore, that the high value of *b* in immature *A. lactifloreus* reflects a general body and gonadal growth which decreases as sexual maturity is attained.

It has been stated above that treatment of *A. lactifloreus* with carbon monoxide has a profound effect on respiratory rate and oxygen consumption. Fig. 5 shows

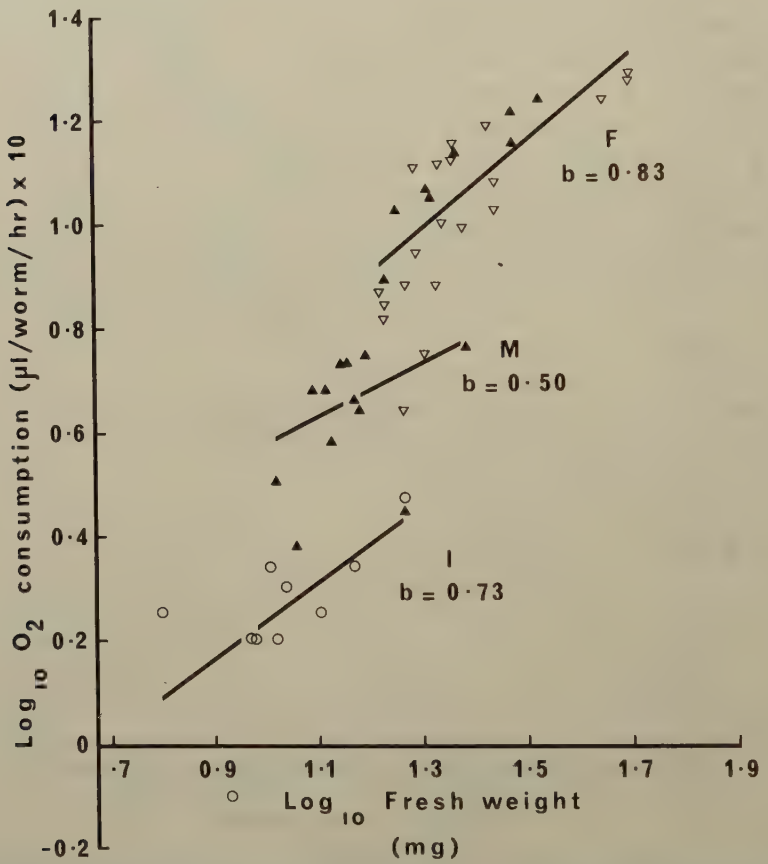

Fig. 5. Double logarithmic$_{10}$ plot of oxygen consumption as a function of body weight: carbon monoxide treated group ($n = 50$); curves were calculated by linear regression analysis; ▽, mature females; ▲, mature males; ○, immature worms.

the double logarithmic plot for oxygen consumption and fresh body weight of *A. lactifloreus* in the presence of carbon monoxide. Three distinct linear regression curves can be fitted to the points, each corresponding to a particular, well-defined, group of animals. Curve I fits a group of 12 individuals, 10 of which were immature.

Curve M fits a group of 12, 10 of which were mature males, and Curve F fits a group of 26 individuals, 18 of which were mature females. It is interesting to compare the *b*-values displayed in Fig. 5 as there is a considerable disparity between all three. Gravid or maturing females have a much higher *b*-value than ripe or maturing males. This trend is not apparent, however, in the absence of carbon monoxide (Fig. 4). Immature animals also have a higher *b*-value than adult males. There is, however, a wide scatter of points for mature males which indicates that no conclusions should be drawn from the apparently low *b*-value depicted. It is essential to note that the actual oxygen consumption values, in the presence of carbon monoxide, are markedly less than those observed in the presence of oxygen alone (Table IV). Table IV also shows that as body weight (size) increases the relative contribution of the respiratory pigment to oxygen consumption decreases. The necessary, and apparently valid (Poluhowich, 1970), assumption is made that low levels of carbon monoxide only interfere with the respiratory pigment and not with any respiratory enzyme system.

TABLE IV

The contribution of an active respiratory pigment to oxygen consumption relative to increasing body weight: 1, see Fig. 4; 2, see Fig. 5, Curve F.

Fresh body wt. (mg)	Fresh body wt. ($\log_{10}$ mg)(1 & 2)	Oxygen consumption $b = 0.72$ (1)	($\mu l\ O_2 \cdot h^{-1}$) $b = 0.83$ (2)	% difference between 1 & 2
15.8	1.20	1.41	0.82	71.95
19.9	1.30	1.68	0.99	69.70
25.1	1.40	1.99	1.20	65.83
31.6	1.50	2.34	1.44	62.50
39.8	1.60	2.79	1.76	58.52
50.1	1.70	3.31	2.14	54.67

The percentage decrease in pigment contribution to oxygen consumption is relatively slight over the live body weight range shown in Table IV. As the majority of nemerteans increase in length rather than in thickness, during growth and development they are able to maintain a high surface area : volume ratio (Mill, 1972). In this way they are able to maintain a high body surface area : nervous system surface area ratio even if body volume increase exceeds nervous system volume increase. As the respiratory pigment occurs within the glial cells of the nervous system and transepidermal diffusion of oxygen is, apparently, the principal respiratory mechanism in the majority of nemertean species, the reason for such a slight loss is apparent when these ratios are considered.

The mechanisms responsible for the different *b*-values exhibited by the three groups of animals in Fig. 5 are not known. It is possible that ciliary beat frequency over the entire respiratory (body) surface could be regulated with respect to the

oxygen demand. Copious amounts of mucus were exuded by some of the individuals during the respirometric procedures. Mill (1972) reported that mucus facilitates oxygen diffusion. At least in *Cyprinus carpio*, however, increasing mucus production on the gills, observed when the fish are stressed, reduces the oxygen consumption per unit weight (Ultsch & Gros, 1979). Presumably there could be a similar situation in nemerteans producing excessive quantities of mucus (Gros, pers. comm.). No information is available to determine whether the males exuded more mucus than the females.

Discussion

The red pigment impregnating the cerebral ganglia and lateral nerve cords of *Amphiporus lactifloreus* has been investigated by means of histochemical, cytochemical and microdensitometric procedures. Cytochemical localization of the oxidized-DAB reaction product has revealed a thermostable peroxidase distributed homogeneously throughout the cytoplasm of certain glial cells. This peroxidase activity persists even after prolonged fixation in neutral-buffered formaldehyde solutions and is unaffected by relatively high (5×10^{-4} to 5×10^{-3} M) cyanide concentrations. Such an ability to split exogenous hydrogen peroxide non-enzymatically has been reported to be characteristic of haemoproteins containing an iron porphyrin prosthetic group (Essner, 1974; Litwin, 1979). It should be made clear, however, that a positive histochemical result for such an activity, obtained by the methods employed here, does not necessarily prove the presence of haemoglobin. Indeed, even the demonstration that ^{55}Fe and tritiated Δ-aminolevulinic acid was taken up and incorporated into various elements of the blood in *Lineus lacteus* (Vernet & Gontcharoff, 1975) does not confirm the occurrence of haemoglobin.

Microdensitometry revealed a rapid change in absorption spectra exhibited by the pigment when anaerobic conditions were induced. The subsequent re-establishment of maxima consistent with normal, aerobic, conditions, in response to an increased oxygen supply, indicates that the pigment is physiologically active. In this respect, and by the fact that the non-enzymic peroxidase activity does not appear to be localized within any one organelle, the pigment resembles that reported by Phillips (1978) surrounding the brain and pharyngeal musculature of *Paravortex scrobiculariae*. Nevertheless, no evidence has been presented, so far, to prove that the absorption spectra were obtained from the substance exhibiting a non-enzymic peroxidase activity. The red pigment, from which the spectral maxima were obtained, occurs, however, in the same glial cells as the "pseudoperoxidase" and both activities are characteristic of haemoproteins. At this point it is interesting to note that the span (in nm) between the α-maxima obtained from pigments in the presence of oxygen and in the presence of carbon monoxide is characteristic of a given haemoprotein (Prosser, 1973a). It is apparent from comparison with other species (Lee &

Smith, 1965; Prosser, 1973a) that the *Amphiporus lactifloreus* pigment (Fig. 3) differs in this respect from any hitherto recorded.

Table III clearly shows that *A. lactifloreus* is able to maintain a constant respiratory rate at low environmental oxygen tensions. It would appear likely, therefore, that this species is a metabolic regulator (Prosser, 1973b). Possibly the concentration or oxygen affinity of the pigment could be regulated (Beadle, 1961) so as to render the oxygen consumption of the worm constant over a wide range of external oxygen levels. The suggestion that the pigment is physiologically active is substantiated by the reduction in respiratory rate and oxygen consumption per worm, by $\approx 50\%$, recorded after treatment with carbon monoxide. A comparable reduction was reported by Poluhowich (1970) after treatment of *Prostoma graecense* with carbon monoxide.

Although no interspecific comparisons for nemerteans were available, Poluhowich (1970) suggested that the respiratory rates of marine nemertean species would be lower than for freshwater species such as *P. graecense*. This was based on the findings of several investigations (Prosser, 1973b) which concluded that the oxygen consumptions of freshwater organisms tended to be higher than those of closely related marine species. Evidence has been provided in this study to corroborate the proposal of Poluhowich (1970). Table II compares the respiratory rates obtained from *P. graecense* with those obtained in the present study. Although there are considerable differences in experimental procedures between the two it is still reasonable to suggest that *P. graecense* has a higher weight-related oxygen consumption (=respiratory rate) than *Amphiporus lactifloreus*. An interphyletic comparison of respiratory rates is presented in Table V. Although the same constraints, regarding experimental conditions, apply to these results there appears to be some degree of similarity between selected representatives of the ectothermic phyla.

TABLE V

Interphyletic comparison of respiratory rates (oxygen consumption per unit live weight): *Amphiporus lactifloreus*, present study; remainder from Prosser (1973b).

Species (Phyla)	Respiratory rate (ml $O_2 \cdot g$ fresh $wt^{-1} \cdot h^{-1}$)	T °C
Amphiporus lactifloreus (Nemertea)	0.072 ± 0.021	14 ± 0.5
Arenicola sp. (Annelida)	0.062	–
Ochestoma sp. (Echiura)	0.069	–
Mytilus sp. (Mollusca)	0.076	15
Carassius sp. (Pisces)	0.077	15
Ambystoma sp. (Amphibia)	0.075	14
Natrix sp. (Reptilia)	0.070	16
Various Mammalia	0.13–10.6	–

Many authors have attributed the presence of a respiratory pigment in invertebrates, particularly in association with the nervous system (Willmer, 1970), to life

in oxygen-poor environments (Poluhowich, 1970; Vernet, 1973; Cahet, 1975). It has been suggested that a store of oxygen near the neural tissue could be useful during periods of low environmental oxygen tensions (Willmer, 1970). As the pigment has been shown to alter its spectral properties immediately on exposure to anoxic conditions, it would seem that the pigment does not act as a long-term store. In fact Kirsteuer (1967) demonstrated that increasing hypoxia exerted a strong influence on the behaviour of many nemerteans. Under such conditions the normal responses of positive geotaxis and negative phototaxis appear to be reversed, as the worms move to the water surface. It is unlikely, in any case, that the whole body respiratory pigment concentration would be sufficient to act as an oxygen store to any significant extent. No conclusion can be drawn at this stage as to the possibility of a catalytic function being afforded by the haemoprotein.

Reference has already been made to the fact that the haem-protein complexes found in the nerves of other marine invertebrates closely resemble mammalian myoglobin. Moreover, it is clear that myoglobin serves to facilitate the transport of oxygen to the mitochondria within the red skeletal muscle fibres so that a local demand can be met instantaneously (Wittenberg *et al.*, 1975; Perutz, 1978). As the central nervous system is extremely susceptible to oxygen deprivation it is reasonable to speculate that a function analogous to that of myoglobin could be attributed to the invertebrate neuro-pigments, especially as Wittenberg (1966) suggested that the facilitation decreases with increasing molecular size of the oxygen-binding proteins.

The present study has reported the homogeneous distribution of an oxidized-DAB reaction product, indicative of the presence of a haemoprotein, within certain glial cells, associated with central nervous neurons, of *A. lactifloreus*. Schindelmeiser *et al.* (1979) reported that glial cells supply metabolic substrates to, and take up transmitters and catabolites from, the neurons they invest. Thus, it would appear possible that the intraglial haemoproteins may function by providing a means by which respiratory gases could be exchanged efficiently at the neuronal surface. In addition, or as an alternative, high intracellular oxygen tensions could be achieved within the central nervous tissue, relative to other body tissues, by the haemoprotein-facilitated diffusion of oxygen. During periods of low oxygen availability the possession of a physiologically active haemoprotein, facilitating the transport of oxygen into and within the central nervous system of *A. lactifloreus*, ensures that a standard cerebral oxygen consumption may be maintained. Reduction in availability of oxygen can occur, (i) as an actual environmental deterioration, e.g. increasing hypoxia due to stagnation or (ii) if a "barrier" is placed between the respiring surface and the external oxygen supply, e.g. if a copious amount of mucus is exuded which would effectively reduce the surface area available for respiration. The latter condition often follows as a result of the former, but has also been observed when the animals are irritated, either chemically or physically. Of importance in this case, as an intertidal organism is being considered, is the production of mucus when *A. lactifloreus* is subjected to salinity stress. Work is at present in progress investigating the in-

volvement of the central nervous tissue in co-ordinating the adaptation and adjustment of the nemertean body when subjected to salinity stress.

In conclusion, it is interesting to speculate that although the cerebral tissue may require a constant level of oxygen supply, the oxygen consumption of other body tissues may conform to the external oxygen levels down to an unknown threshold.

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DISTRIBUTION AND POPULATION DYNAMICS OF THE LIMPET *PATELLA VULGATA* L. IN BANTRY BAY

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Abstract: The population ecology of *Patella vulgata* L. was studied as part of an oil pollution baseline study. The reproductive cycle was determined; recruitment, growth, and mortality were studied in detail in nine populations, and samples were collected at up to four tidal levels on a variety of shores. Maturation of the gonads began in July–August and spawning was in late September 1972 and in January–February 1974. Recruitment was influenced mainly by the wetness of the habitat. There was little evidence of annual fluctuations in recruitment success, except on a local scale. Growth rate and maximum length attained were highest on bare rock and lowest among closely packed barnacles. Growth was also favoured by wet conditions. Changes with time in growth rate and size attained were related to changes in biological habitat. There was very little seasonal variation in growth rate. Mortality was divided into juvenile and adult phases. Juvenile mortality was very great in wet sites but somewhat less in the presence of fucoids. On dry sites with barnacles, there were fewer juveniles and these lived longer and suffered less mortality. Most adult limpets died of old age, and longevity and growth rate appeared to be inversely related. During the period of study, there was a net loss of limpets from the nine populations being considered in detail.

Changes in numbers $\cdot m^{-2}$, wet weight $\cdot m^{-2}$, and mean length by weight were related to tidal level and exposure to wave action. Much variation was encountered in these and in length-frequency distributions: this was related, in part, to changes in biological habitat, but temporal changes also seemed to be important. Population structure reflected population history.

With increasing exposure to wave action, *P. vulgata* is almost totally replaced by *P. aspera*. On exposed shores, the two species grow at similar rates and *P. aspera* appears to become dominant because it suffers less mortality among juveniles. At low tidal levels, the growth rate of *P. aspera* does not change with increasing shelter, but *P. vulgata* grows faster and becomes the dominant limpet species. At higher tidal levels the growth rate of *P. vulgata* is less variable, and the distribution of *P. aspera* seems to be limited by its greater susceptibility to desiccation. The better survival of juveniles of *P. aspera* may be a critical factor in the development of high-density, small-size populations at the presumed centre of its range.

Cyclical changes between limpets and fucoids appeared to be in progress on some of the shores investigated, and it is argued that certain shores are incapable of supporting a stable limpet population; on a very local scale there are continual fluctuations. The absence of the southern species *P. depressa* may be a critical factor in this.

The ability of the survey to detect subtle long-term changes is briefly discussed. Temporal change and instability are the main unpredictable factors affecting the results, and the survey would be improved by continued regular surveillance.

INTRODUCTION

The work described here forms the major part of a base-line study of Bantry Bay, southwest Ireland, where an oil transshipment terminal was opened in 1968. The

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limpet *Patella vulgata* L. is a "girder", "keystone" or "foundation" species, as defined by Elton (1966), Paine (1969), and Dayton (1972). It is also very susceptible to pollution by oils and dispersants (Crapp, 1971b, c, d). It was reasoned, therefore, that long-term ecological changes, arising from oil pollution, were most likely to be detected through changes in limpet populations (cf. Southward & Southward, 1978). Also, a plan based upon limpet populations was relevant to wider studies of littoral ecology and surveillance, in addition to being well directed to the detection of subtle change (Lewis, 1970, 1976, 1979; Bowman, 1978). The work was based upon a general survey of the shores of Bantry Bay (Crapp, 1973), and studies on the limpet *Patella aspera* have already been described (Thompson, 1979).

Although much work has been done on the population biology of *P. vulgata*, most recently by Lewis & Bowman (1975), it is not yet possible to predict the distribution of population types over the full range of natural habitats, except in very general terms. This is the major obstacle to using *P. vulgata* as an indicator of damage by oil pollution; the present survey is, therefore, based upon collections of limpets taken from a variety of shores in Bantry Bay, covering different tidal heights, exposure to wave action, and biological habitats. In order to interpret the results, regular observations were also made on nine selected populations for periods of one year or more, the reproductive cycle was determined, and additional collections were made to explore variations in population structure on a very local scale.

For the purpose of long-term population surveillance, comprehensive records have been deposited with the Department of Agriculture and Fisheries in Dublin, and with the Department of Zoology in University College, Cork.

Materials and Methods

Limpets were collected from up to four tidal levels (M.L.W.N., M.T.L., M.H.W.N., M.H.W.S.) at a series of stations described by Crapp (1973) and graded into exposure categories, using a modification of the scale of Ballantine (1961a), ranging from extremely exposed (Grade 1) to extremely sheltered (Grade 8). Stations were numbered after Crapp (1973): e.g., Station 3.5 is the fifth station in exposure Grade 3. Normally one square metre was sampled by removing all limpets from four 50 × 50 cm squares. Random sampling was not practicable because of the irregular surfaces and heterogeneous environments encountered, and care was taken to avoid sampling from a mixture of habitats that obviously differed in character. The characteristics of the habitat were carefully recorded in each case. In the laboratory, the shell length of all limpets was measured to the nearest mm and the total wet weight, including shells, was determined in each mm class.

From these various populations, nine were selected for further study, as described in Table I. The sites at Reenydonagan and Gurteenroe were located 1 km apart at the eastern end of Bantry Bay: those at Iskanafeelna and Relane were 5 km to the

northeast and southeast, respectively. In each case, two 50 × 50 cm squares were marked out with paint, except at Iskanafeelna M.T.L. and Iskanafeelna M.H.W.N. Flat, where four squares were established. All limpets in the squares were measured to the nearest 0.1 mm shell length, using vernier callipers, and animals of 15 mm shell length or more were individually marked with spots of enamel paint. The positions of the marked animals were recorded using a quadrat grid. The sites were re-visited every 2 months, except when bad weather intervened, and the measurements were

TABLE I

Patella vulgata: habitats and periods of observation in the nine selected populations.

Name of site	Exposure grade	Tidal level	Habitat	Period of observation	
				Start	Finish
Iskanafeelna	4	M.T.L.	Barnacles on a gentle slope, changing to barnacles and fucoids, mainly *Fucus vesiculosus*	21 Mar. 1972	10 Sept. 1973
Iskanafeelna	4	M.H.W.N.	Barnacles on a FLAT surface, changing to barnacles and fucoids, mainly *Fucus vesiculosus*	15 Apr. 1972	10 Sept. 1973
Iskanafeelna	4	M.H.W.N.	Barnacles on a STEEP surface facing south	5 July 1972	10 Sept. 1973
Reenydonagan	5	M.L.W.N.	Bare rock and mussels on a gentle slope	7 Dec. 1971	21 Mar. 1973
Reenydonagan	5	M.T.L.	Barnacles and mussels on a gentle slope	7 Dec. 1971	21 Mar. 1973
Relane	5–6	M.T.L.	Bare rock and fucoids, mainly *Ascophyllum nodosum*, on a moderate slope facing south	15 July 1972	11 Sept. 1973
Gurteenroe	6	M.L.W.N.	Bare rock and fucoids, mainly *Fucus serratus*, on a gentle slope	1 July 1972	2 July 1973
Gurteenroe	6	M.T.L.	Barnacles on a flat but uneven surface	17 Apr. 1972	26 Nov. 1973
Gurteenroe	6	M.H.W.N.	Barnacles on a flat but uneven surface	1 July 1972	2 July 1973

repeated and the marks renewed. At the end of the experimental period, all the limpets were removed and taken to the laboratory for determination of wet weights.

In studies of the reproductive cycle, samples of *P. vulgata* were collected from four 50 × 50 cm squares at Bocarnagh Bay, on the northern coast of Bantry Bay. It proved difficult to find suitable sampling areas after the first three collections, and after January 1973 samples of 100 *P. vulgata* (minimum length 31 mm) were taken instead. By September 1973 so many limpets had been collected that a new site was required, and sampling was transferred to a shore of similar aspect, slope, and exposure at Dereenacarrin, 4 km to the west. From 26 September to 22 November, samples were taken alternately at the two sites, and after that, from Dereenacarrin alone. In the laboratory, gonad condition was assessed using the index of Orton *et al.* (1956).

Results

GONAD CONDITION

The gonad index is shown in Fig. 1. There were no significant differences between males and females and the index does not differentiate between them. In 1972, the index reached a mean value of no more than 4 before falling between 27 September and 22 November. In 1973, spawning apparently was at some time between 31 De-

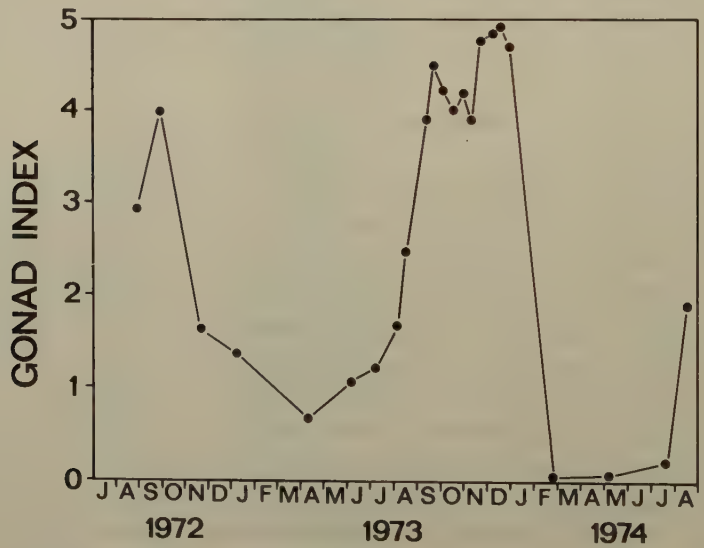

Fig. 1. Gonad index for *Patella vulgata*: up to November 1972 the index is based upon all animals >21 mm, collected from one m^2 at M.T.L. at Bocarnagh Bay, numbers vary from 29 to 43 animals; after January 1973 the index is based upon collections of 100 limpets >31 mm; in October and November 1973, samples are alternately from Bocarnagh Bay and Dereenacarrin; from December 1973 they are from Dereenacarrin alone.

cember 1973 and 25 February 1974. Maturation of the gonads began in July–August in 1973 and 1974.

RECRUITMENT IN THE NINE SELECTED POPULATIONS

Limpets of <15 mm shell length were too small to be marked successfully but it was normally possible to identify year-classes by length-frequency analysis. The method of Taylor (1965) was used, applying a moving average of three. A χ^2 test for goodness of fit was used to compare the sums of the component curves (without the moving average) with the observed distribution, and the results were accepted as not being significantly different when $P > 0.05$. The method was not extended to the larger animals because in these, overlapping between the sizes of different year classes made it impossible to arrive at an unambiguous result.

Examples of length-frequency analyses are shown in Fig. 2. In the two populations at M.H.W.N. at Iskanafeelna, very young limpets were rarely found. On the Flat site, one to three animals <12 mm were usually present, but their lengths varied and they appeared to be migrating in and out of the area. On the Steep site, animals <12 mm were normally absent, and the population appeared to be sustained by immigration. Evidence of this was noted on 24 June 1973 when four new animals, of 10, 14, 18, and 18 mm shell length, appeared in the two squares.

Also shown in Fig. 2 are two populations which showed marked changes in length-frequency distribution over the period of study. At Iskanafeelna M.T.L., these variations seemed to be associated with changes in the biological habitat. In 1972, the rock was dominated by an even cover of barnacles, at a density of ≈ 200 *Balanus balanoides* (L.), 40 *Chthamalus stellatus* (Poli), and 20 *Elminius modestus* Darwin dm^{-2}. By 6 June 1973, however, 23% of the surface was covered by sporelings of *Fucus vesiculosus* L., 5–10 cm long. These grew during the summer and, on 10 September, 47% of the surface was covered by plants 8–15 cm long. It appeared, therefore, that this site was changing from one dominated by barnacles, to one covered by fucoids and the surviving patches of barnacles, and the limpet population was changing with it. This will be discussed later. A similar invasion by *F. vesiculosus* was also seen at the M.H.W.N. Flat site at Iskanafeelna where 26% of the surface was covered by weed on 24 June 1973, increasing to 58% by 10 September. In the latter case, however, there were no obvious changes in the limpet population.

At Gurteenroe M.T.L., the population was initially dominated by animals of the 1970 year class, as shown in Fig. 2. By April 1973, however, numbers in this class had decreased to a level typical of other year classes.

Numbers in each recognizable year class, derived from length-frequency analysis, are shown in Fig. 3 for several sites. Year classes are designated by the year immediately following their spawning: i.e. the 1973 class was spawned in autumn 1973, and the 1974 class in early 1974. In general, three patterns can be recognized: (1) early appearance of the juveniles, with numbers reaching a peak by July, as at

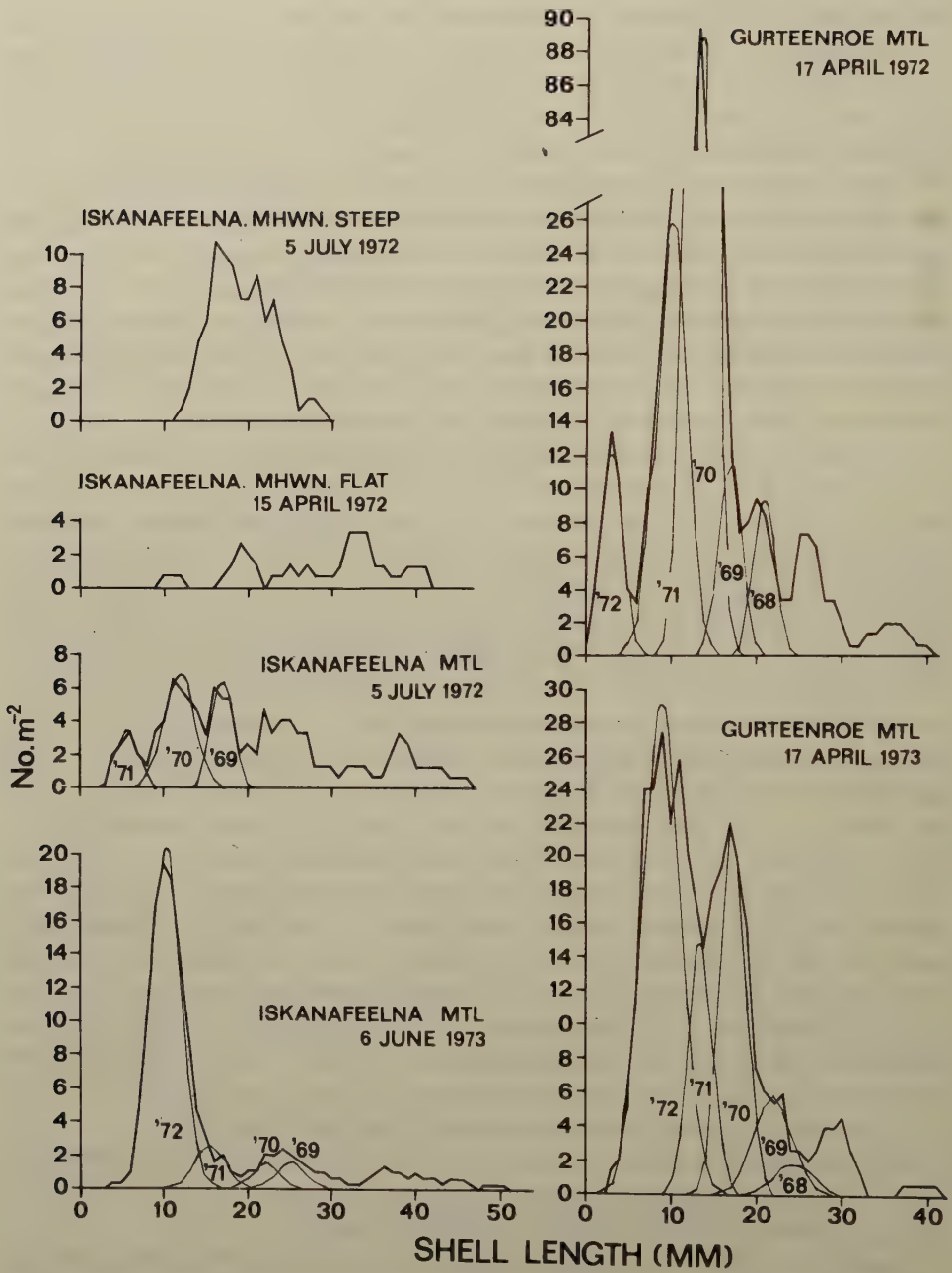

Fig. 2. Length-frequency distributions of *Patella vulgata*: examples from four selected populations, as discussed in the text; a moving average of three is applied both to the overall distributions (thick lines) and to their component normal curves (thin lines); year classes are indicated where these could be defined.

M.L.W.N. at Reenydonagan and Gurteenroe, and at M.T.L. at Relane; (2) late appearance of the juveniles, with numbers reaching a peak in the period December–March, more than one year after spawning, as at M.T.L. at Iskanafeelna, Reenydonagan, and Gurteenroe; (3) very low numbers of juveniles with little evidence of a seasonal peak, as at M.H.W.N. at Gurteenroe. This last pattern also applies to

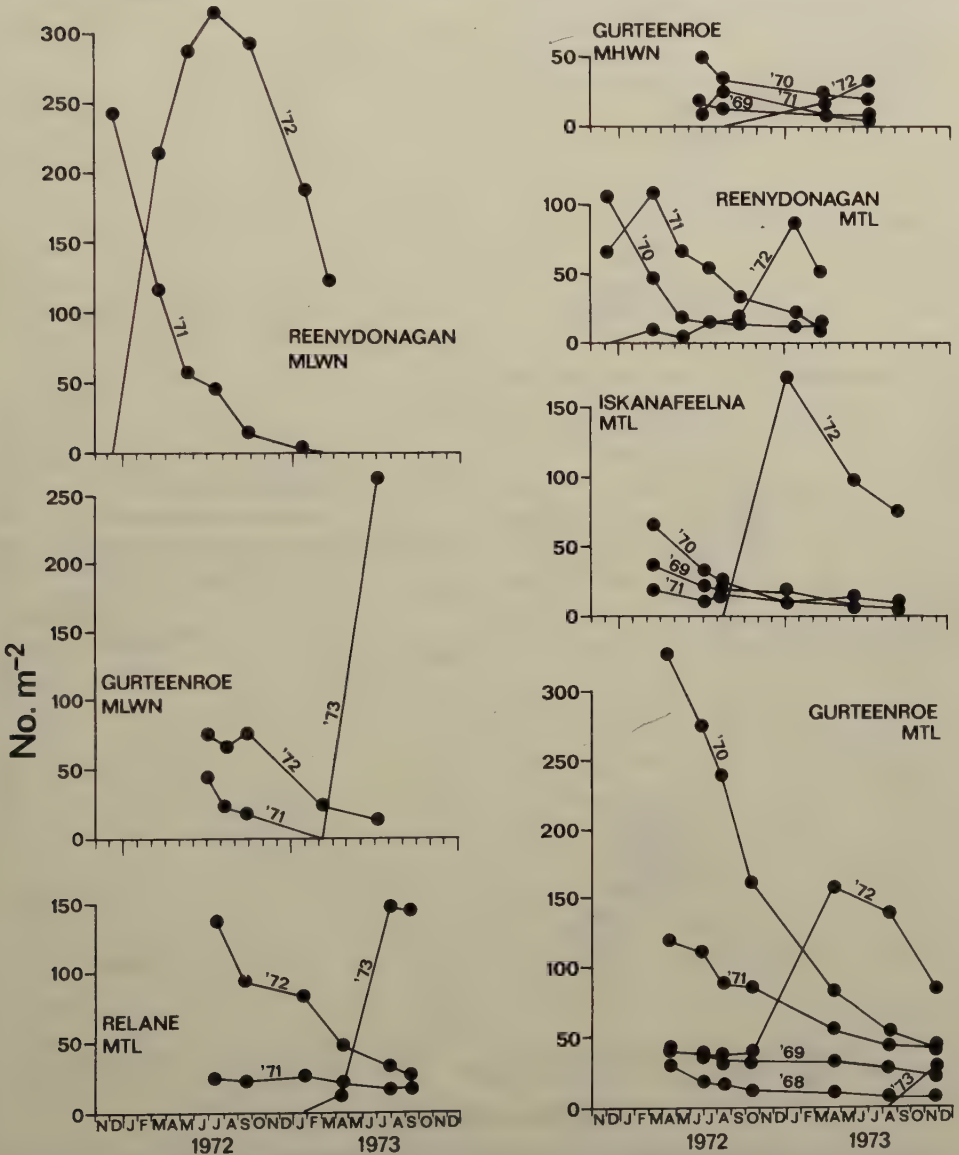

Fig. 3. Numbers of *Patella vulgata* in each recognizable year class, derived from length-frequency analysis, in seven populations.

the two M.H.W.N. sites at Iskanafeelna, where there were too few juveniles for year class identification.

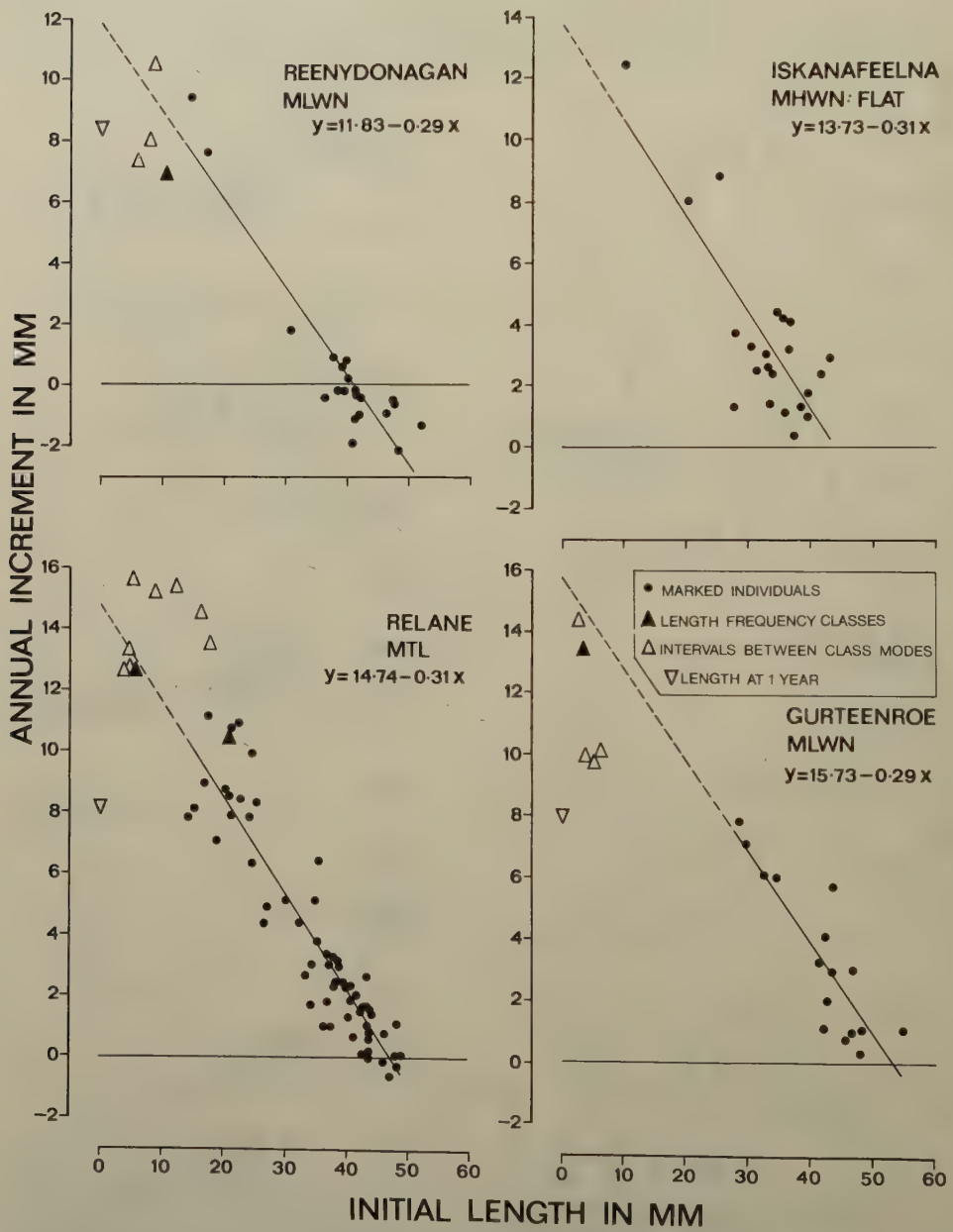

Fig. 4. *Patella vulgata*: annual increments of shell length in four populations; regression lines, calculated by the method of least squares, are based on marked individuals only and extrapolated lines are dashed; for all lines, correlation coefficients r are significant at $P < 0.05$.

GROWTH OF THE NINE SELECTED POPULATIONS

Four methods were used to estimate growth: (1) annual increments of marked individuals; (2) annual increments in length-frequency classes; (3) intervals between class modes in length-frequency analyses; and (4) the size of the youngest class after

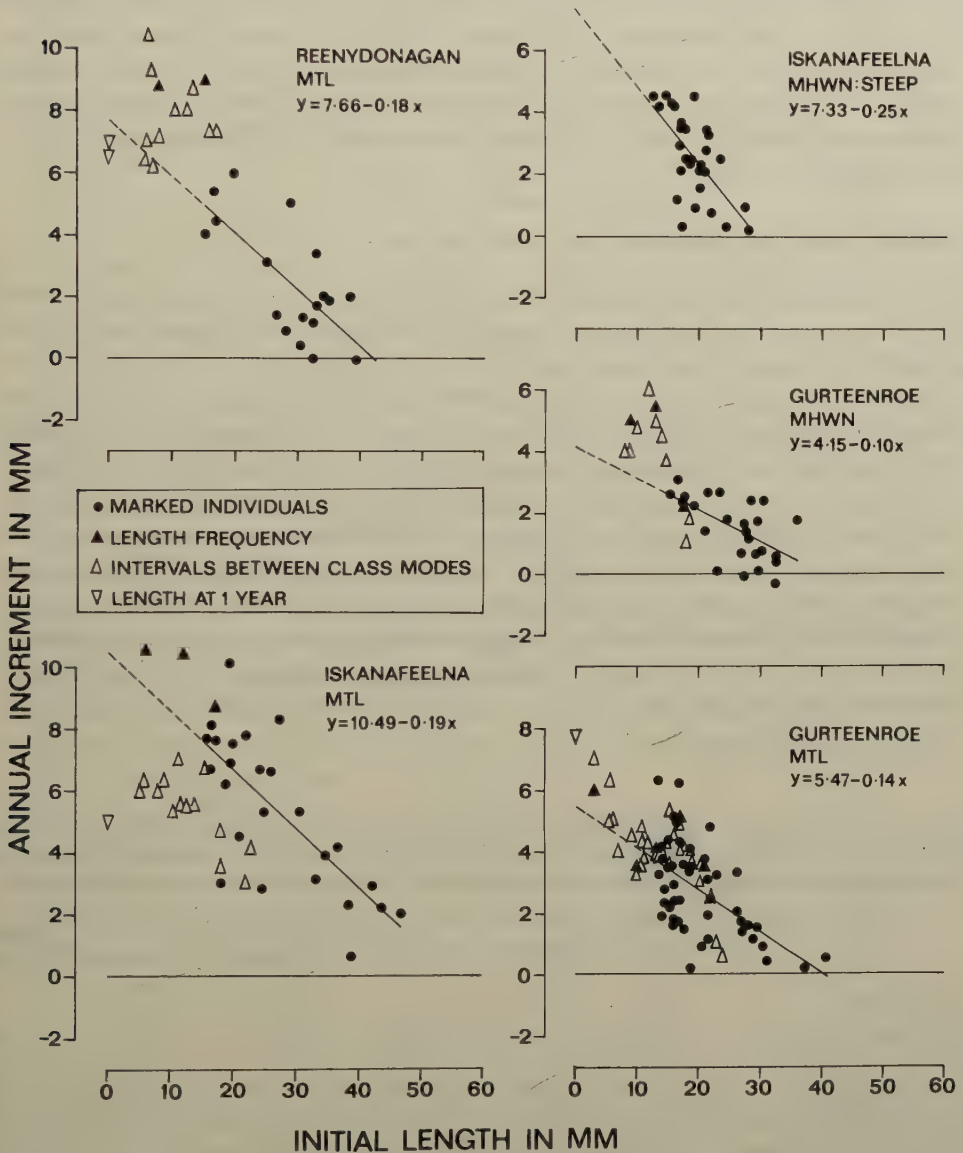

Fig. 5. *Patella vulgata*: annual increments of shell length in five populations; regression lines, calculated by the method of least squares, are based on marked individuals only and extrapolated lines are dashed; for all lines, correlation coefficients r are significant at $P < 0.05$.

one year, assuming spawning on 1 January. Of these four methods, only the first is entirely satisfactory, and these data alone have been used to calculate the regression lines shown in Figs. 4 and 5. The results of the other three methods are shown, however, for comparison. In all populations, growth rates were inversely proportional to initial length. There were substantial differences in growth rates between populations, and these are discussed later. Growth continued through all seasons, but in some populations there was an indication of slower growth during the winter, particularly at M.L.W.N. at Reenydonagan, where there was a negative mean increment in shell length of marked individuals for autumn 1972. This is ascribed to shell erosion among the large individuals that comprised this population (cf. Fig. 4 and Ballantine, 1961b).

MORTALITY IN THE NINE SELECTED POPULATIONS

The main difficulty in assessing mortality is that individuals may migrate away from the marked site but do not necessarily die. Sometimes a marked dead shell was found, trapped by mussels or barnacles encroaching upon it, but more often a missing limpet could be found, alive and healthy, on rocks up to 2–3 m away from the original square. Mortality patterns are, therefore, best examined by dividing the limpets into four groups: (1) limpets remaining in the same place for a full year; (2) limpets remaining alive but moving away from their original home and in some cases outside the marked area; (3) limpets originally present but disappearing over the course of a year (including those found dead); and (4) limpets appearing during the year, either by growing past the 15 mm "cut-off" length for marking, or by immigrating into the square. Results are summarized in this way in Table II, for animals >15 mm length for one full year; normally the year following the start of observations was used, but some sites were not re-visited after exactly one year, and a later period was used instead.

TABLE II

Patella vulgata: migration and mortality over a 12-month period in the nine selected populations, with details of net gain or loss in numbers, all as percentages of the total number (n) of marked individuals >15 mm length; sites ranked by increasing percentage of limpets remaining in the same place (see text for further details).

Name of site	n	Remained	Moved	Disappeared	Appeared	Net gain or loss
Gurteenroe M.T.L.	115	10	16	37	37	0
Reenydonagan M.L.W.N.	33	12	46	36	6	−30
Gurteenroe M.L.W.N.	44	16	20	41	23	−18
Iskanafeelna M.T.L.	81	17	10	47	26	−21
Gurteenroe M.H.W.N.	55	29	16	44	11	−33
Reenydonagan M.T.L.	39	33	5	49	13	−36
Iskanafeelna M.H.W.N. Flat	33	42	21	30	6	−24
Relane M.T.L.	95	51	15	13	21	+8
Iskanafeelna M.H.W.N. Steep	42	52	10	26	12	−14

At the two wet, low-level sites, M.L.W.N. at Gurteenroe and Reenydonagan, very few limpets remained on a single home for the full year, and there was much movement of limpets within and in and out of the marked squares. In drier habitats, migration became less common, and more than 50% of the limpets remained in one place at Iskanafeelna M.H.W.N. Steep and Relane M.T.L. Since the latter site was on bare rock bordered by *Ascophyllum nodosum* (L.) Le Jol., a trend against movement is not simply a function of dry habitats with barnacles. There was an apparent exception to the general trend at Gurteenroe M.T.L., where only 10% of the limpets remained stationary in a dry habitat, but this reflected the influence of large numbers of animals in the 1970 year class. In this, there were heavy losses among animals 15–20 mm long at the start of the year, but many more grew, on-site, past the 15 mm "cut-off" point for marking during the course of the year.

There was a net decrease in limpet numbers at all sites except M.T.L. at Relane and Gurteenroe, and this raises the question of whether the manipulation and marking of the limpets itself contributed to mortality. This will be discussed later, but reference may be made here to an interesting sequence of events noted at Relane M.T.L. Two 50 × 50 cm squares were first set up on 15 July 1972, adjacent to each other, and these were re-visited on 14 September. In the first square, three limpets >15 mm shell length had disappeared out of a total 23. In the second square, 14 limpets >15 mm had disappeared or died (one marked but empty shell remained in place) out of a total 19. These mortalities occurred after the first marking of the limpets but they were nearly all in only one of the two squares, and such mortalities were not observed again or in any other marked area: thus, it is unlikely that the marking contributed to the mortalities. The sudden reduction in the numbers of larger limpets is suggestive of a group of predators roaming past; the remaining dead shell had been bored by the dogwhelk *Nucella lapillus* (L.). Because numbers in the selected population were greatly reduced, two new squares were established on 14 September and the results from all four squares have been used in the preparation of Table II, starting from 14 September.

It may be concluded, therefore, that mortality patterns in the limpet populations cannot be assessed unless migratory patterns are also understood, and a single year, which may or may not be typical, is too short a period for determination of how and when the limpets die. In one instance, mortalities over a 2-month period differed by 3/23 compared with 14/19 in two adjacent squares.

DISTRIBUTION AND ABUNDANCE IN BANTRY BAY

Samples of *Patella vulgata* were collected from all the stations described by Crapp (1973) except for two sites with an exposure rating of 4 (4.4 and 4.10) and the four most sheltered sites (7.4, 8.1, 8.2, 8.3). Sampling was confined to the four tidal levels M.H.W.S., M.H.W.N., M.T.L., and M.L.W.N. (cf. the distribution pattern shown in Crapp, 1973) and all limpets were counted and weighed (including shells).

Some collections were repeated, normally because the site in question was re-visited for another purpose. Results are shown in Fig. 6. At M.L.W.N. the number · m^{-2} rose from exposure Grade 1 to exposure Grade 5, and then decreased again in greater shelter. Wet weight · m^{-2} increased in the same way from Grade 1, but remained high through Grades 5 to 7. At M.T.L., numbers and weights were

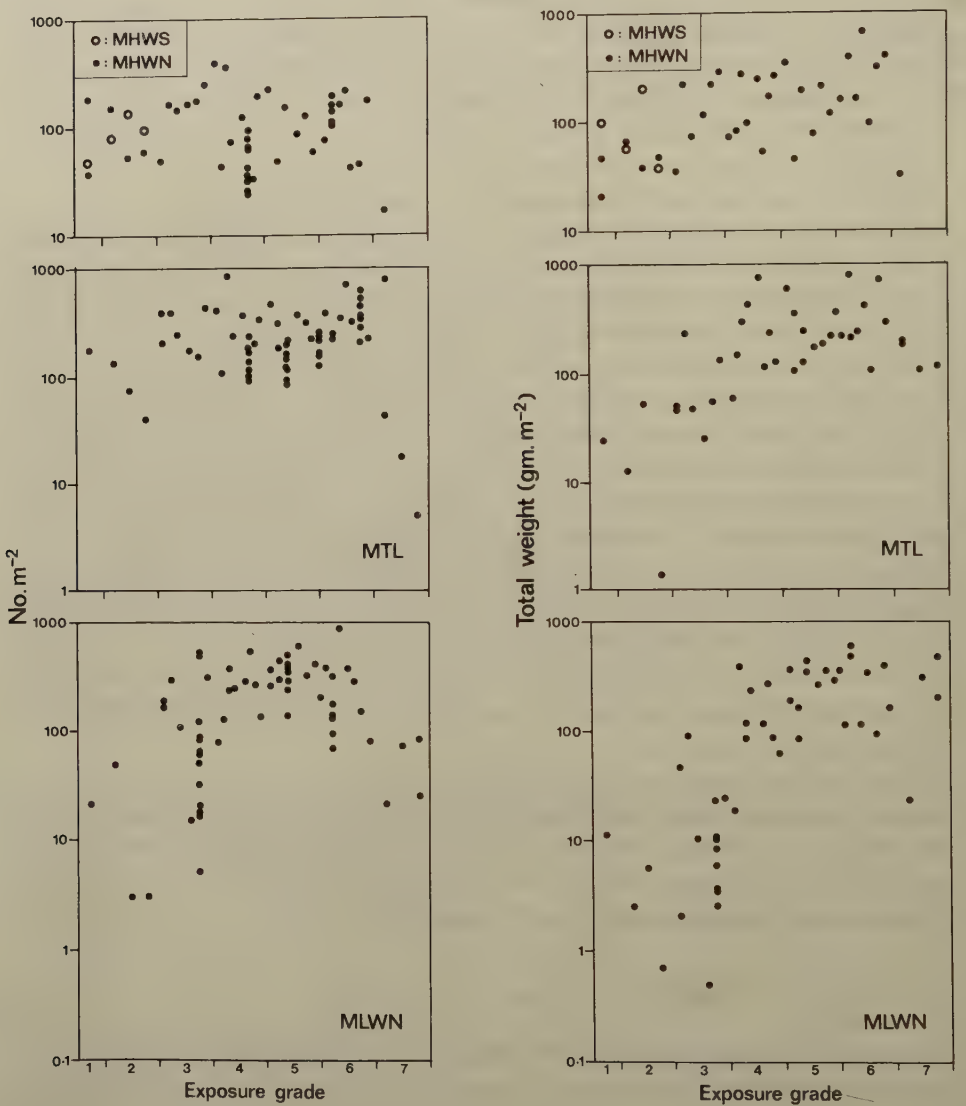

Fig. 6. Total numbers and wet weights of *Patella vulgata* · m^{-2} at 34 sites and four tidal levels in Bantry Bay, in relation to exposure to wave action: some sites were sampled more than once, and numbers recorded in the experimental populations are also included.

similar to those at M.L.W.N. on Grades 4 to 6, except that numbers declined less markedly on more exposed shores. Numbers declined abruptly on Grade 7 shores but weights showed a smaller drop. At M.H.W.N. these trends were continued; numbers and weights decreased very little on more exposed shores, and the decline on Grade 7 shores was so marked that samples could not be found on two of them.

The mean size of the adult limpet population may be expressed as mean length

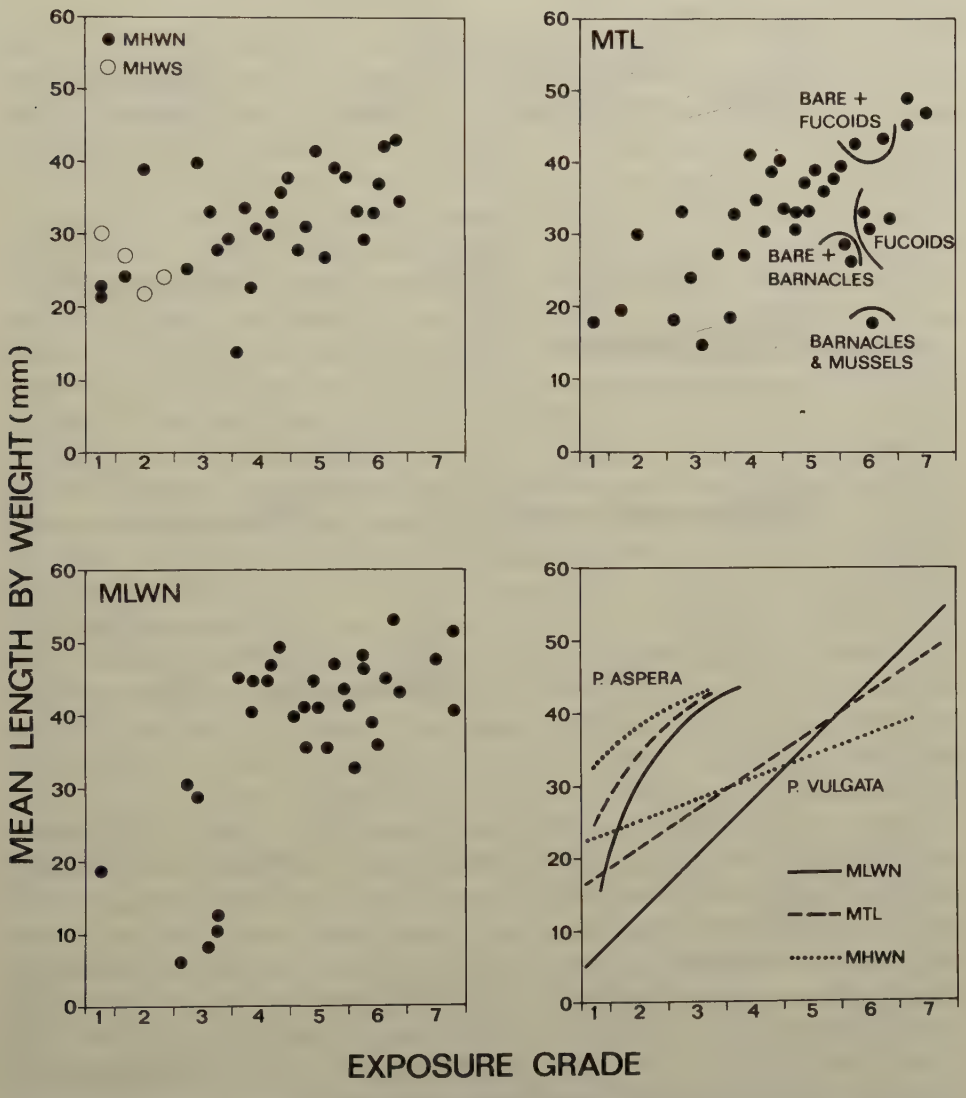

Fig. 7. Mean lengths by weight of *Patella vulgata* at 34 sites and four tidal levels in Bantry Bay, in relation to exposure to wave action: at bottom right, major trends are compared with those reported for *P. aspera* by Thompson (1979).

by weight, estimated by plotting accumulative weight against length and recording the length at which 50% of the total weight is reached (Ballantine, 1961b; Lewis & Bowman, 1975). For *P. vulgata*, mean lengths by weight are shown in Fig. 7 for all populations in which there were sufficient numbers of limpets for data analysis. The general trend at each tidal level is from smaller sizes in exposed areas to larger sizes in shelter, but this is less marked at high tidal levels. Hence in exposure, the largest limpets are found at M.H.W.N. and M.H.W.S., but in shelter the highest limpets tend to be the smallest.

There is much variability in these results. Numbers $\cdot m^{-2}$ are very sensitive to the numbers of juveniles present, while wet weight $\cdot m^{-2}$ is greatly influenced by the numbers of large animals that happen to be present in the m^2 sampled. Both numbers and weights, and mean lengths by weight, are much influenced by variations in biological habitat; this is most obvious in the results for mean length at M.T.L. in Grade 6. As shown in Fig. 7, the largest mean lengths by weight were found on bare rock patches with some fucoid cover. Smaller mean lengths were found on rocks with very dense fucoid cover, on bare dry rocks, and among barnacles. The smallest mean size was found in a population living among mussels and patches of densely packed barnacles. Lewis & Bowman (1975) have shown the importance of biological habitat in determining population structure in *P. vulgata*, and typical variations in length-frequency distributions are shown, for the present survey, in Figs. 8, 9, and 10.

At M.L.W.N. (Fig. 8), exposed shores were dominated by bare rock with a variable cover of mussels, except at Site 1.1 where there was a 95% cover of the kelp *Alaria esculenta* (L.) Grev. over mussels. In Grades 1 and 2, the limpet population was always dominated by *Patella aspera*, and *P. vulgata* were rare and small. On Grade 3 shores a more variable pattern was found; *P. vulgata* might be completely dominated by *P. aspera* (Site 3.4), or the two species might be co-dominant (Site 3.2), or intermediate patterns might be found (Site 3.3). On Grade 4 shores the two species were always co-dominant. Here, it became possible to find sites without mussels; these always had a bare surface but the absence of mussels did not seem to affect the limpet populations (cf. Sites 4.3 and 4.7). On Grade 5 shores *P. vulgata* always dominated the limpet populations (cf. Fig. 10 in Thompson, 1979).

Fucoids, mainly *Fucus serratus* L., became important on some Grade 5 shores, but their influence was difficult to assess. Mean length by weight was not consistently greater or smaller in the presence or absence of fucoids (cf. Sites 6.5, 6.6, 5.5, and 5.6). It was arguable that mean length was reduced under dense fucoid cover, where bare rock was eliminated (cf. Site 5.4 with 5.6, and 6.4 with 6.6) but comparable variations in mean length could also be found among bare rock sites (cf. Sites 6.1 and 6.5) or between bare rock and bare rock and mussels sites (cf. Sites 5.2 and 5.5).

On Grade 7 shores, the dominant feature at all sites was the great reduction in numbers of juveniles, whether fucoids were present or not.

At M.T.L. (Fig. 9), much habitat variation was introduced by the presence or absence of *Fucus vesiculosus*. Where the surface was dominated either by mussels

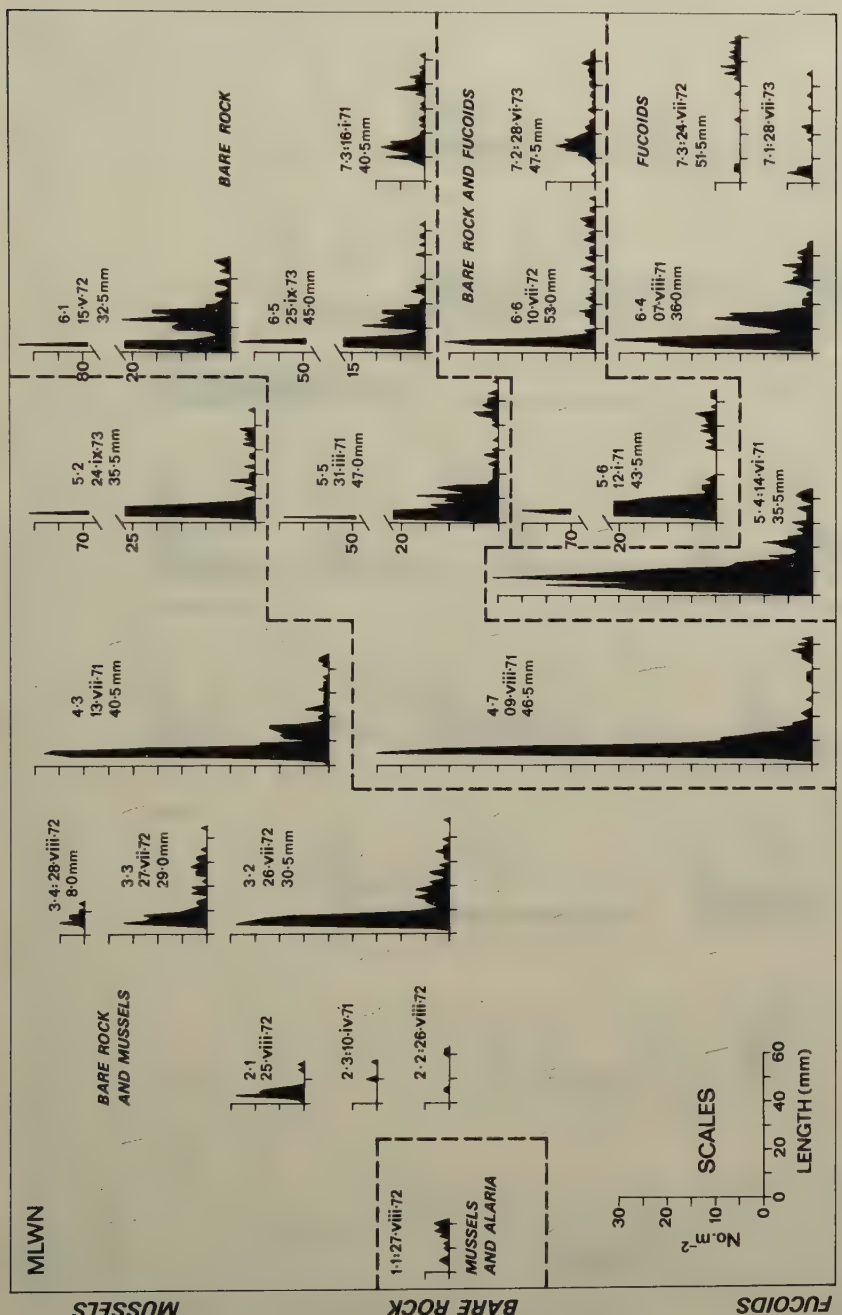

Fig. 8. Variations in length-frequency distributions for *Patella vulgata* at M.L.W.N., in relation to biological habitat and exposure to wave action: site number, sampling date, and mean length by weight are given for each example; site number denotes exposure grade (last digit) and rank within grade (2nd digit); see text for further details.

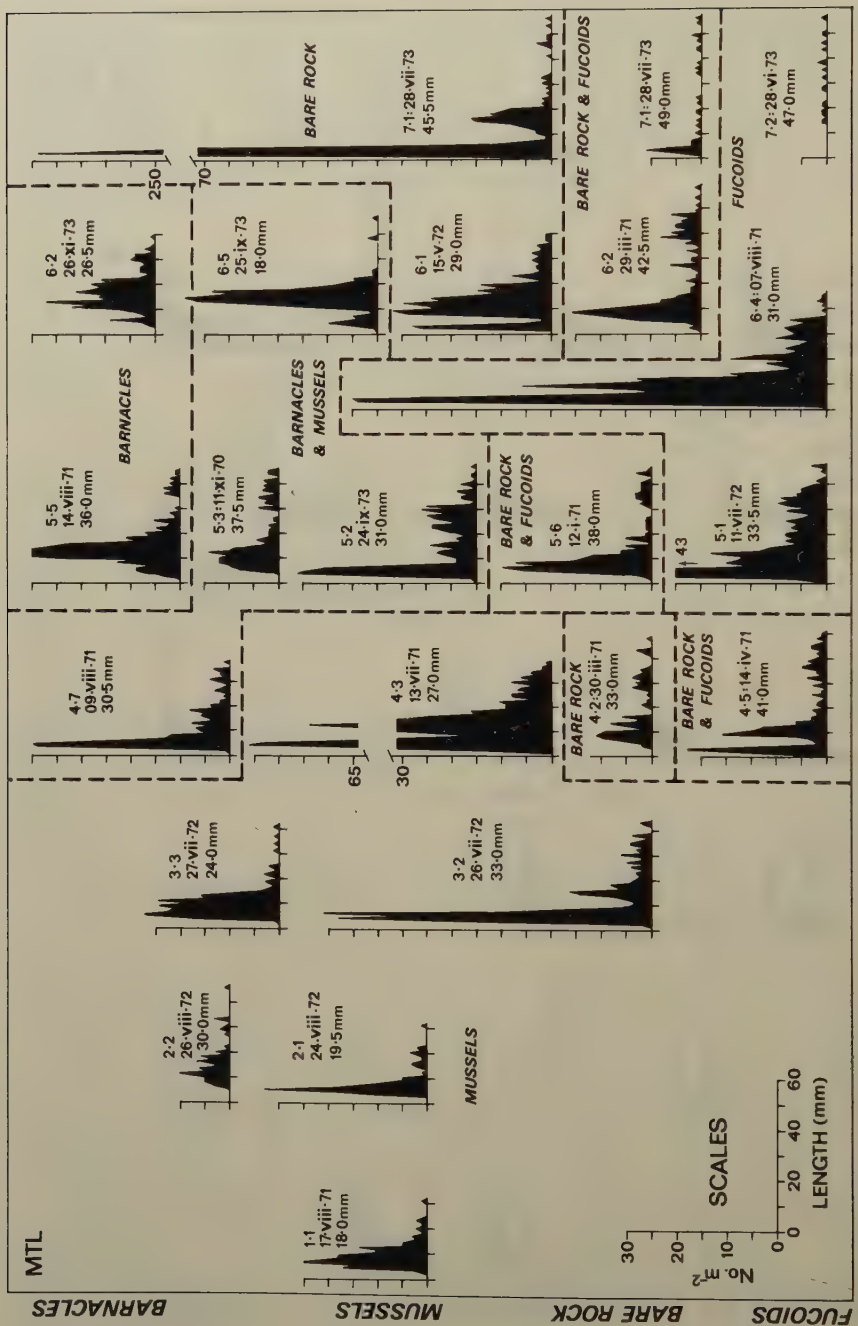

Fig. 9. Variations in length-frequency distributions for *Patella vulgata* at M.T.L., in relation to biological habitat and exposure to wave action: site number, sampling date, and mean length by weight are given for each example; site number denotes exposure grade (1st digit) and rank within grade (2nd digit); see text for further details.

or by barnacles and mussels, the extent of fucoid cover did not seem to affect the limpet population and, in Fig. 9, variations in fucoid cover have been ignored for all habitats where mussels were important.

On exposed shores, the presence of mussels was always the most important factor at M.T.L., and the damp areas close to them contained many juvenile limpets. On Grades 1 and 2, *Patella aspera* was always the dominant limpet; on Grade 3 *P. aspera* and *P. vulgata* were co-dominant. On shores of Grade 4 onwards, *P. aspera* were scarce or absent, and *P. vulgata* was the dominant species of limpet.

Barnacles became important on Grade 4 shores, but usually in combination with mussels. Perhaps because of this, little change was apparent in the limpet distributions (cf. Sites 3.2 and 4.7). There were very few mussels in the selected site at Iskanafeelna M.T.L., which was dominated by barnacles, and the low numbers of young limpets probably reflected the lack of damp areas (see Fig. 2). On bare rock the numbers of juveniles also seemed low, although this could have been a seasonal effect as the site was sampled in March (Site 4.2). Juveniles were more numerous under *Fucus vesiculosus*, where mean length by weight was also greater (Site 4.5).

On shores of Grades 5 and 6, sites dominated by barnacles alone were common, and these appeared to have slow-growing, late-emergence populations, typified by the selected population at Gurteenroe M.T.L. (Site 6.2). Where mussels were also present, juveniles were more numerous but mean length by weight remained quite low (cf. Sites 5.5, 5.3, and 5.2). The selected population at Reenydonagan M.T.L. represented this type. The population at Site 6.5 was unusual in that very few large *Patella vulgata* were found. There was little apparent difference between populations on bare rock and those among barnacles and mussels (cf. Sites 6.1 and 5.2) but there was some evidence that populations on bare rock around fucoids (as at Relane M.T.L.) had greater mean lengths by weight (cf. Sites 6.2, 6.1, 5.6, and 5.2). Under denser fucoids, however, where there were no bare surfaces, mean lengths by weight again decreased, partly because of better survival among young limpets (Sites 5.1 and 6.4).

On Grade 7 shores, total numbers of limpets $\cdot m^{-2}$ were usually low, the sole exception being a vertical, north-facing wall at Site 7.1. This population contained a very large number of juvenile *P. vulgata*, and a few *P. aspera* were also present. The sample was characteristic of more exposed shores, and the reasons for its appearance in Grade 7 are not clear.

At M.H.W.N. (Fig. 10), interpretation of the pattern of population structures becomes more difficult. For example, among dense barnacles, a common length-frequency distribution was that found in the selected populations at Iskanafeelna M.H.W.N. Steep (see Fig. 2) and Gurteenroe (Site 6.2, and Sites 5.1, 4.3, and 4.6). Nevertheless, in the same habitat, quite marked variations from this pattern could be found (Site 4.1). Similarly, marked variations could be found in the bare rock and mussels habitat at Grade 3 (Sites 3.1, 3.5, 3.6, 3.4, and 3.3).

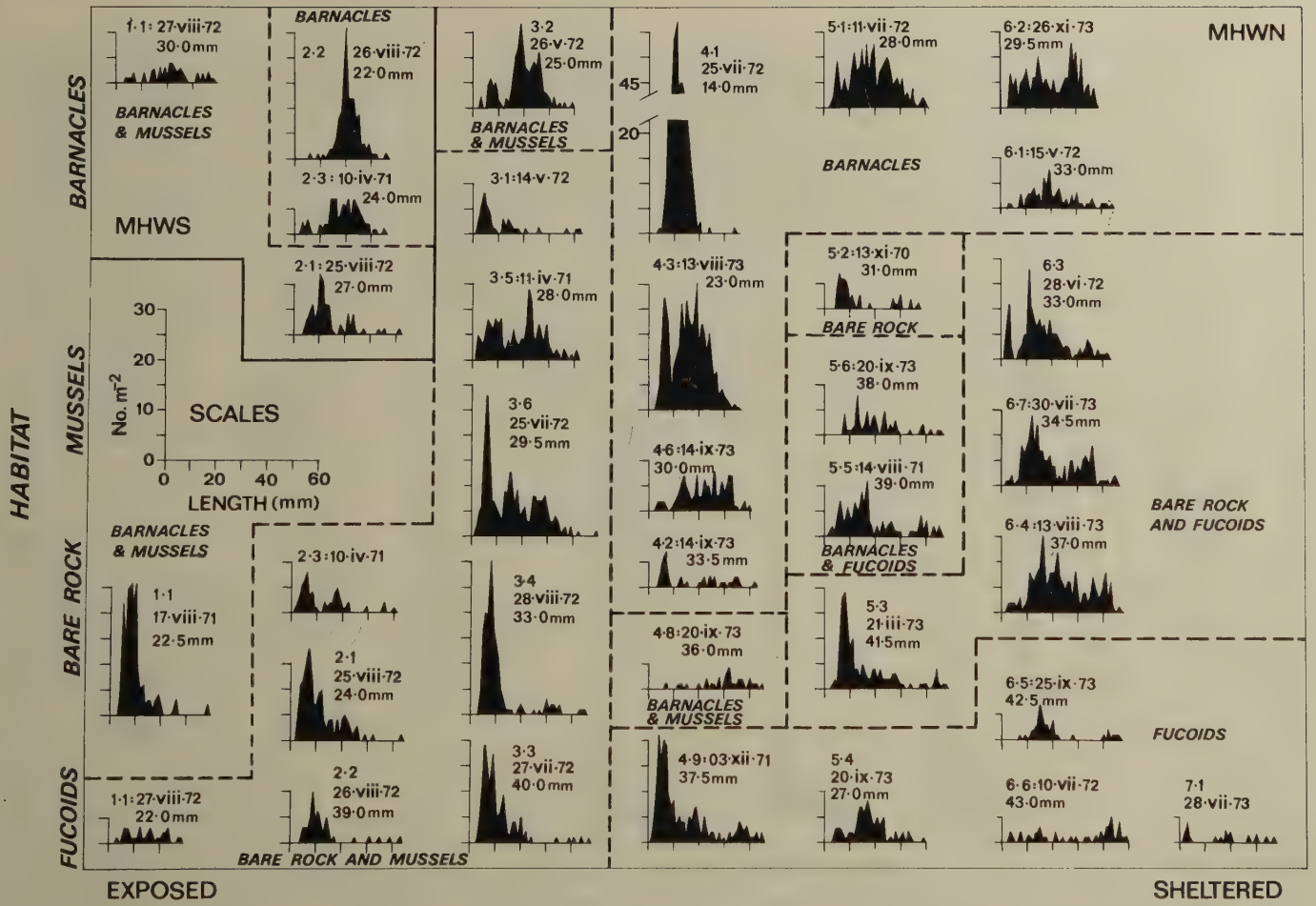

Fig. 10. Variations in length-frequency distributions for *Patella vulgata* at M.H.W.N. and M.H.W.S., in relation to biological habitat and exposure to wave action: site number, sampling date, and mean length by weight are given for each example; site number denotes exposure grade (1st digit) and rank within grade (2nd digit); see text for further details.

It is still possible, however, to identify an overall pattern. On Grades 1 and 2, *P. aspera* dominated the limpet population, but Grade 3 shores were very variable. At Sites 3.3 and 3.4, *P. aspera* comprised 64–67% of the total weight of *Patella*. This decreased to 31% at Site 3.1 and to 1–2% at Sites 3.2, 3.5, and 3.6. On more sheltered shores, *P. aspera* was rarely found at this tidal level. On exposed shores, bare rock and mussels was the normal habitat, and the mussels seemed to provide shelter for juveniles, although fewer juveniles were found here than at lower tidal levels. On sheltered shores, there was often a clear distinction between some of the barnacle dominated shores and sites covered by fucoids (Sites 4.9, 6.5, and 6.6) but this was not always so (cf. Sites 4.6 and 5.4). Where there was bare rock around the fucoids, *P. vulgata* was more abundant, but not necessarily larger (Sites 6.3, 6.7, 6.4, and 5.3). Numbers of *P. vulgata* generally fell when barnacles were abundant under fucoids (Sites 5.6 and 5.5), and also on bare rock (Site 5.2).

At M.H.W.S. (Fig. 10), limpets were only found on Grades 1 and 2, and *P. aspera* formed 80% of the total weight of *Patella* at Sites 1.1 and 2.1, 7% at Site 2.2 and 0% at Site 2.3. The habitat was usually dominated by barnacles (Sites 2.2, 2.3, and 2.1) but mussels were also present at Site 1.1.

From these observations, it may be concluded that the pattern of population distribution in *P. vulgata* is mainly accounted for in terms of exposure to wave action and tidal level, but that biological habitat is an important modifying factor. The greatest numbers of *P. vulgata* were found in populations with an abundance of juveniles, at low tidal levels on shores of intermediate exposure. Numbers decreased on more exposed and more sheltered shores, at higher tidal levels, and in drier habitats. The largest animals were found at low tidal levels on sheltered shores. Variations in biological habitat were smallest on very exposed and very sheltered shores and at low tidal levels, and greatest at mid-level sites on shores of intermediate exposure. Mussels and fucoids provided shelter for young limpets; barnacles did not. At higher tidal levels, marked differences became particularly noticeable between populations living in the same biological habitat, at the same tidal level and exposure grade. Although these could arise from unnoticed differences in habitat, it will later be suggested that they originate in differences in the biological history of each site.

LOCAL HABITAT VARIATION AND CHANGES WITH TIME

As this investigation progressed, it became increasingly clear that the limpet population of a given area was by no means constant and immutable in the long term. This emerged through the study of the nine selected populations, notably at Iskanafeelna, but it was also apparent on other shores. Typically, some areas were dominated by limpets and others by fucoids, and to illustrate the differences, collections of limpets were taken from three M.T.L. populations at each of two sites. These were a Grade 4 shore at Dereenacarrin, in a small bay, and a Grade 6 shore

at Ardnagashel, near the head of Bantry Bay. All samples were from one m^2 on gently sloping rocks facing southeast, and were taken from local patches of rock, several m^2 in extent, having distinctive types of fucoid cover. Length-frequency distribu-

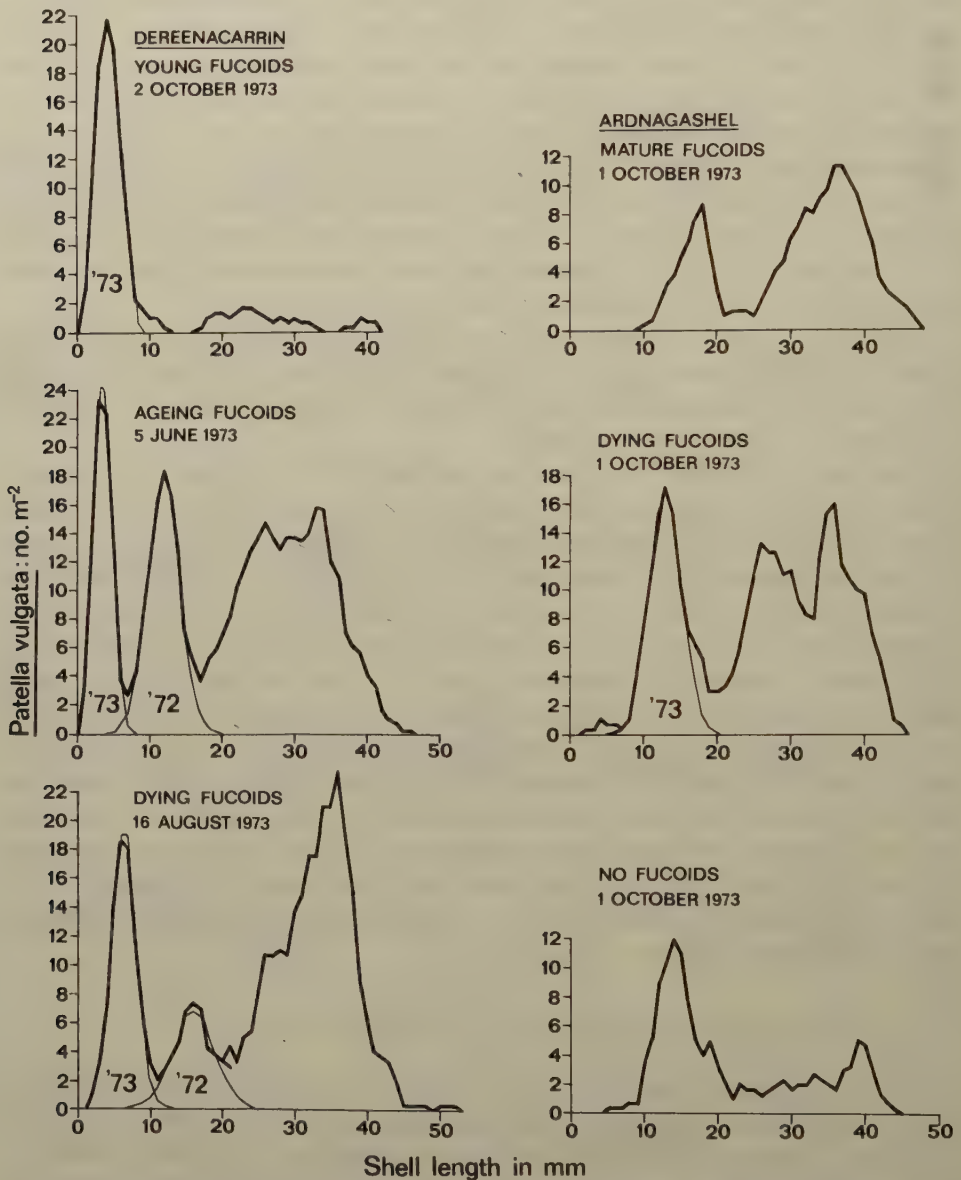

Fig. 11. Length-frequency distributions of *Patella vulgata* from different biological habitats at M.T.L. at Dereenacarrin and Ardnagashel: a moving average of three is applied both to the overall distributions (thick lines) and to their component normal curves where identified (thin lines); year classes are indicated where these could be defined.

tions are shown in Fig. 11 and the fauna and flora of the six habitats are listed in Table III.

TABLE III

Fauna and flora of the six habitats sampled at Dereenacarrin and Ardnagashel.

	Dereenacarrin			Ardnagashel		
	Young fucoids	Aging fucoids	Dying fucoids	Mature fucoids	Dying fucoids	No fucoids
P. vulgata						
$g \cdot m^{-2}$	46.0	827.7	1264.6	1088.4	1273.3	348.4
no. $\cdot m^{-2}$	119	439	392	180	332	132
mean wt (g)	0.4	1.9	3.2	6.0	3.8	2.6
mean length by wt (mm)	33.0	33.0	35.0	37.0	36.0	38.0
Fucus vesiculosus						
$g \cdot m^{-2}$	9000.5	4415.9	493.4	3554.8	62.8	0
no. $\cdot m^{-2}$	351	246	49	52	3	0
mean wt (g)	25.6	18.0	10.1	68.4	20.9	–
% cover	100	72	5	50	2	0
Ascophyllum nodosum						
$g \cdot m^{-2}$	0	0	0	6409.4	406.6	0
no. $\cdot m^{-2}$	0	0	0	36	12	0
mean wt (g)	–	–	–	178.0	33.9	–
% cover	0	0	0	50	5	0
Balanus balanoides						
adults: no. $\cdot dm^{-2}$	1–10	<1	0	<20	40	400
spat: no. $\cdot dm^{-2}$	1–10	300–500	100–300	–	–	–
Chthamalus stellatus						
no. $\cdot dm^{-2}$	1–10	0	10–200	0	<1	80
Mytilus edulis						
% cover	30	1	3	0	0	0
Actinia equina						
no. $\cdot m^{-2}$	10	10	0	0	0	0
Gastropods, no. $\cdot m^{-2}$						
Gibbula umbilicalis	45	185	0	0	0	4
Littorina littorea	55	298	0	1	0	52
L. littoralis	10	22	5	12	0	0
Nucella lapillus	134	70	0	0	0	95

In each habitat, all of the fucoids present were of the same size, appearance and, presumably, age (cf. Knight & Parke, 1950). No area supported a mixed population with different age groups represented. The different populations can, therefore, be arranged in a series, according to the type of fucoid cover, as follows: young fucoids, mature fucoids, ageing fucoids, dying fucoids, no fucoids. The young fucoids, sampled at Dereenacarrin, were immature plants of *Fucus vesiculosus* f. *linearis*

Huds., 15–30 cm long, lying flat upon the rock. The mature plants were 20–30 cm long, sturdy with well developed stipes and forming a canopy 10–20 cm high. The dying fucoids formed a similar canopy, but the plants had a worn and tattered appearance, and their mean weight had declined from 18.0 to 10.1 g (Table III). At Ardnagashel, the fucoids consisted of a mixture of *F. vesiculosus* and *Ascophyllum nodosum*. The mature plants were, in the case of *Fucus vesiculosus*, 30–45 cm long, declining to tattered stipes 10–15 cm in the dying population. Mature *Ascophyllum nodosum* were 30–80 cm long, declining to stumps of 10–15 cm in the dying population.

In animals other than *Patella vulgata*, numbers varied greatly between the different habitats, as shown in Table III. These variations probably reflect the amount of shelter provided by the fucoid canopy but they are not considered in detail. In *P. vulgata*, the populations differed mainly in the biomass and abundance of large animals. The older the fucoids appeared to be, the greater was the biomass of the limpets (Table III). At Dereenacarrin, there were also marked differences in the survival of the 1972 year class, but these could be explained by mortalities occurring over the period June–October (Fig. 11).

These observations suggest that conditions were more favourable for limpet survival under the algal canopy than on bare rock, permitting a large population to become established over a period of several years. Because the algal canopy apparently consisted of no more than a single age group in each habitat, it must eventually disappear. The large population of adult limpets might then survive for some time, but the favourable conditions under which it became established would no longer apply. Thus, these populations are inevitably unstable and have a limited life.

Discussion

THE REPRODUCTIVE CYCLE

The reproductive cycle in *P. vulgata* has been studied by numerous workers, notably Orton *et al.* (1956). The most recent, and comprehensive, study is that of Bowman & Lewis (1977) at Robin Hood's Bay and elsewhere. The latter authors confirmed earlier work, in that there was normally a single sharp fall in the gonad index in October or November, and spawning was apparently triggered by rough seas. An important finding of this work was, however, that different years may be characterized by different patterns of spawning. In 1972, the spawning pattern at Robin Hood's Bay was almost identical to that shown for Bantry Bay for the same year in Fig. 1; spawning took place as soon as maturation was complete but the gonad index remained quite high for some time afterwards. In 1973, spawning patterns were quite different. In both places there was a small index drop during September gales, indicating a minor and premature spawning. At Robin Hood's Bay this was

followed by the main spawning in early October, but in Bantry Bay the main spawning did not take place until some time in early 1974. The latter pattern was identical to that observed at Robin Hood's Bay in 1969.

If the present results are compared with those reported for *P. aspera* in Bantry Bay by Thompson (1979), it appears that *P. aspera* matures and ripens one or two months before *P. vulgata*. Whether or not the two species spawn together depends upon the chance occurrence of rough weather. In 1972, the autumn gales were unusually late, at the end of October. *P. aspera* had been fully mature for two months but *P. vulgata* had only just reached maturity, and both species spawned together. In 1973, spawning in *P. aspera* was apparently triggered by gales at the end of September, but there was only a slight fall in the gonad index of *P. vulgata*, which did not show a major decrease until three or more months later.

These observations agree with those of earlier workers (Orton *et al.*, 1956; Branch, 1974a; Bowman & Lewis, 1977; Thompson, 1979), who supposed that the spawning stimulus only becomes effective when a certain stage of maturation is reached. Since the gonad index was higher before the subsidiary spawning of September 1973 than before the main spawning of October 1972, this stage may be related to timing rather than to gonad size.

RECRUITMENT IN THE SELECTED POPULATIONS

Variations in the recruitment of *P. vulgata* have been discussed by several authors (e.g. Hatton, 1938; Fischer-Piette, 1948; Jones, 1948; Ballantine, 1961b). All agree that the very young limpets require a damp habitat and are least numerous on dry rocks with barnacles and under dense fucoids. A more detailed account was given by Lewis & Bowman (1975), who emphasize the importance of subtle factors such as the presence of small, shallow, damp depressions in the rock. They showed that there is a clear distinction between wet "direct settlement" sites and dry "late emergence" sites. The present results agree closely with those of Lewis & Bowman, although it may be noted that numbers of young were almost always greater on the Bantry shores than in the area of Robin Hood's Bay.

Bowman & Lewis (1977) proposed that recruitment in *P. vulgata* was controlled initially by desiccation acting immediately after settlement, followed by the chance incidence of frost during the following 3 to 5 wk, with major fluctuations in recruitment success depending mainly on the latter hazard. This appears to be true for Robin Hood's Bay and other northern localities, but it is unlikely to apply in Bantry Bay, where frosts are rare. This was recognized by Bowman & Lewis, who predicted that recruitment should be consistently good in southwestern regions. The present results were not intended to be a way of testing this prediction, and it is obvious from Fig. 3 that substantial variations in recruitment success can exist on any one site. Nevertheless, when all the survey results from low- or mid-level wet, direct settlement habitats are combined, rejecting the seasonally low values from

TABLE IV

Patella vulgata: no. · m $^{-2}$ in four different year classes in low or mid-level wet, direct settlement habitats; results are ungrouped data from various sites in summer and autumn, arranged within each year class by date of collection; *n*, number of observations.

	Year class			
	1970	1971	1972	1973
	446	266	189	501
	356	340	209	676
	416	259	529	272
	375	346	222	272
	212	496	264	200
	168	187	219	
	397	372	256	
		290		
n	7	8	7	5
Mean	339	320	270	384
SD	106	93	117	199

winter and spring, it appears that the prediction of Bowman & Lewis is probably true; as shown in Table IV, there is little evidence of widespread annual fluctuations in recruitment.

GROWTH IN THE SELECTED POPULATIONS

Growth rates have been determined for *P. vulgata* by numerous authors, notably Russell (1909), Orton (1928), Hatton (1938), Fischer-Piette (1939, 1941), Ballantine (1961b), Choquet (1968), and Blackmore (1969a). The most recent account is that of Lewis & Bowman (1975), and their conclusions agree closely with the present results. In particular, they argued that growth rate and maximum length attained were highest on bare rock and least among closely packed barnacles. For the present data, this is clearly shown in the growth curves of Fig. 12, which are derived from the regression lines given in Figs. 4 and 5. The curve for the Iskanafeelna M.H.W.N. Flat population is, however, an exception to this. The designation of this habitat as "barnacles" is, perhaps, misleading. Barnacles were the dominant organism, at densities of up to 300 *Balanus balanoides* and 100 *Chthamalus stellatus* · dm $^{-2}$, but they were distributed in patches. It is possible that "bare rock and barnacles" would be a more accurate designation, and this would account better for the growth curve. Lewis & Bowman supposed that the differences between bare rocks and rocks with barnacles probably reflected the ease with which moving and grazing could be accomplished. The configuration of the barnacle populations, in terms of obstructions to limpet grazing, may be more important than absolute density. In Fig. 13, the present results are summarized and compared with those of Lewis &

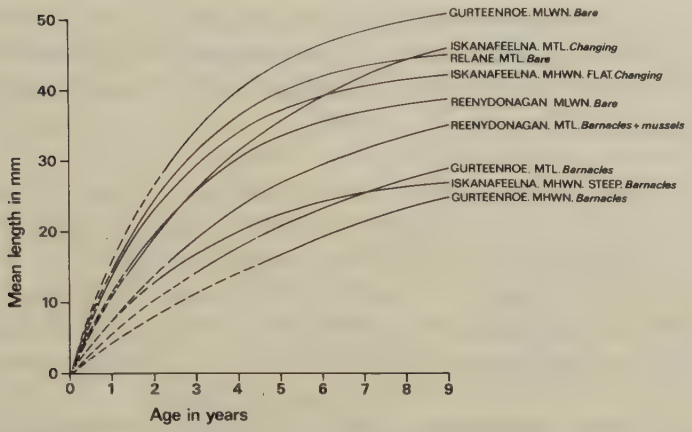

Fig. 12. Mean growth of *Patella vulgata* in the nine selected populations: curves are based on the regression lines in Figs. 4 and 5, and extrapolated lines are dashed.

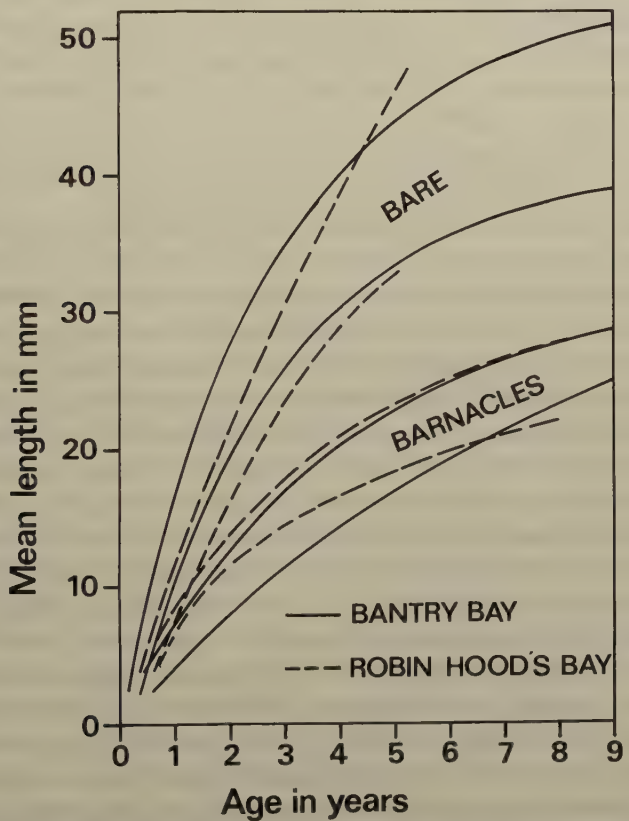

Fig. 13. Maximum and minimum growth of *Patella vulgata* in bare rock and barnacle-dominated habitats in Bantry Bay and Robin Hood's Bay: data for Robin Hood's Bay are from Lewis & Bowman (1975).

Bowman for bare rocks and rocks with barnacles, and a close agreement is apparent. For clarity, the growth curve for Reenydonagan M.T.L. is omitted; if included, it would coincide with Lewis & Bowman's curve for a mid-level barnacle and mussel habitat, also omitted.

Lewis & Bowman emphasized the strong influence of biological habitat upon growth and pointed out that changes in the surrounding species would produce corresponding changes in the limpet populations. This happened at Iskanafeelna M.T.L., where fucoids invaded the site, and it is interesting to note that the growth curve for this population cuts across those adjacent to it in Fig. 12. This implies that growth was unusually great in the older animals, as might happen under changed conditions. Such changes in growth were not apparent, however, at Iskanafeelna M.H.W.N. Flat, despite a similar invasion by fucoids.

Patella vulgata does not hibernate in winter (Blackmore, 1969b), although Barry & Munday (1959) found that blood glucose levels were low in winter, and several authors have reported that growth is slower in winter compared with summer (Russell, 1909; Orton, 1928; Ballantine, 1961b; Choquet, 1968; Blackmore, 1969a; Lewis & Bowman, 1975). This is most obvious in colder regions; Hatton (1938) reported that growth was regular throughout the year in Brittany, and there were no more than small indications of a winter reduction in growth in the present results.

MORTALITY AND LONGEVITY

Mortality in *P. vulgata* may be divided into juvenile and adult phases. As was pointed out by Lewis & Bowman (1975), juvenile mortality is inextricably bound up with recruitment processes, and is complicated by differences between populations in the time of emergence, and also immigration and emigration. A general distinction may, however, be drawn between wet, direct settlement sites, which support large numbers of short-lived juveniles, and dry, late emergence sites, characterized by smaller numbers of juveniles which are more likely to live longer. The differences are summarized, as survival curves, in Fig. 14. These are not true survival curves; the data were collected over too short a period and numbers in several year classes have been placed in sequence, on the assumption that they were originally equal (see Fig. 3). This is a dangerous assumption and in fact, the 1970 year class at Gurteenroe has been excluded because it is an obvious exception. It is also impossible to provide a true origin for survival curves in *P. vulgata*, and the curves in Fig. 14 start, like those of Lewis & Bowman (1975), on the date when maximum numbers of juveniles were recorded, even though this differs from one population to another. Subject to these limitations, the following important conclusions may be drawn from the three selected curves shown in Fig. 14. (i) At Reenydonagan M.L.W.N., juveniles disappeared completely at the beginning of their third year. (ii) The curve for Relane M.T.L., at first indistinguishable from that for Reenydonagan M.L.W.N., begins to flatten in 2-yr-olds and survival is still about 10% towards the

end of the third year. This suggests that, whatever factor was responsible for this mortality, its effects were mitigated, at least at low densities, by the presence of fucoids. (iii) At Gurteenroe M.T.L. there was a substantial juvenile mortality, but this occurred 8–12 months later than at the two wet sites, and levelled out at 20–30% survival.

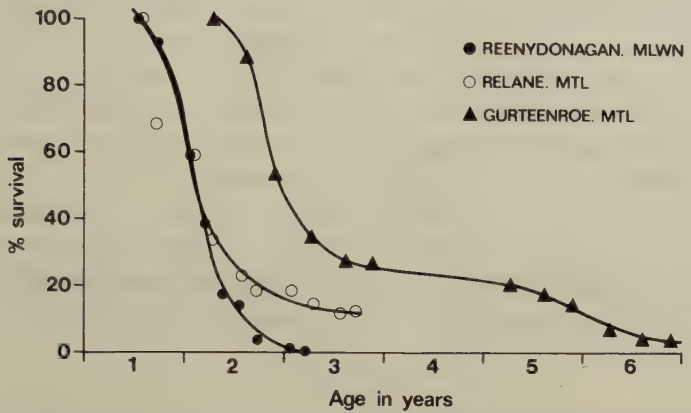

Fig. 14. Tentative survival curves derived from numbers of *Patella vulgata* in recognizable year classes, as shown in Fig. 3: curves have been derived from several year classes placed in sequence, on the assumption that numbers were originally similar in each one; data from the 1970 year class at Gurteenroe M.T.L. have been omitted; see text for further details.

The cause of these juvenile mortalities is not clear, and it will be further discussed in the context of competition between *P. vulgata* and *P. aspera*.

Predation appears to be an erratic and local influence on adult *P. vulgata*. Lewis & Bowman (1975) state that the major detected predator is the oyster catcher *Haematopus ostralegus* L., as described by Feare (1971). Feare found that the birds preferred the larger limpets and took *P. aspera* more often than *P. vulgata*. Most attacks were made on the anterior of the limpet, where the adductor muscle is weakest: *P. aspera* appeared to be more vulnerable because its anterior end is more distinctive than that of *P. vulgata*, and its shell is more easily broken. Lewis & Bowman found that, because oyster catchers feed in small flocks, their influence was very local and erratic. The birds were not responsible for any regular and widespread pattern of adult mortality, but they could exert catastrophic effects on specific groups of limpets. This kind of predatory behaviour could well account for the sudden disappearance of limpets from Relane M.T.L. described earlier.

Shells of *Patella vulgata* were sometimes found drilled by the dogwhelk *Nucella lapillus*. This predation has not been studied in detail, but is probably similar in principle to the predation of *Dicathais aegrota* on *Patelloida alticosta*, described by Black (1978). On Bantry Bay shores, *Nucella lapillus* is abundant but patchily

distributed in groups; a maximum density of 1150 was recorded in a single m^2 at Dereenacarrin. Nevertheless, although a roaming group of *N. lapillus* could, potentially, destroy a population of *Patella vulgata*, the proportion of drilled shells was quite low in groups of dead shells. *Nucella lapillus* appeared to be feeding mainly upon barnacles and mussels, taking limpets only occasionally.

These observations agree with those of earlier workers, who have concluded that most adult *Patella vulgata* die of old age, and that longevity is inversely related to growth rate (Fischer-Piette, 1939, 1948; Ballantine, 1961b; Lewis & Bowman, 1975; cf. Ginet, 1966). Branch (1974b) makes the important point that senescence may become critical in different ways. In *P. oculus* and *P. longicosta*, the oldest animals are unable to repair the edge of the shell and so maintain a close fit with the substratum, and they then become vulnerable to predation. It is difficult to estimate longevities from the present results, which extend over little more than one year, but some conclusions may be drawn from comparisons of the maximum lengths predicted from growth data, the maximum lengths observed, mean lengths by weights, and the number of years needed to reach the latter, as shown in Table V. (1) Maximum

TABLE V

Patella vulgata: maximum lengths predicted from growth data in Figs. 4 and 5, maximum lengths observed, mean lengths by weight, and number of years required to reach the mean length, in the nine selected populations; sites ranked in order of growth rates.

Name of site	Maximum predicted length (mm)	Maximum observed length (mm)	Mean length by weight (mm)	No. of years to reach mean length by weight
Gurteenroe M.L.W.N.	53.3	56.0	46.5	6
Iskanafeelna M.T.L.	54.8	48.8	36.5	5
Relane M.T.L.	46.9	49.4	39.5	5
Iskanafeelna M.H.W.N. Flat	44.0	45.8	39.0	6
Reenydonagan M.L.W.N.	41.0	52.3	41.0	–
Reenydonagan M.T.L.	42.2	41.0	33.0	8
Gurteenroe M.T.L.	40.1	41.1	26.5	8
Iskanafeelna M.H.W.N. Steep	29.4	28.2	22.0	5
Gurteenroe M.H.W.N.	40.4	41.5	29.5	12

observed lengths were within 1–3 mm of predicted lengths, except at Iskanafeelna M.T.L. and Reenydonagan M.L.W.N. At the former site, the maximum length predicted was 6 mm greater than that observed, and this may be ascribed to the presumed increase in growth rate at this site, discussed earlier. At the latter site, the maximum length predicted was 11.3 mm less than that observed and in fact, the predicted maximum length and the mean length by weight were identical. The limpets appeared to be growing more slowly than before, for unknown reasons. A similar discrepancy was noted by Ballantine (1961b) in one of his four selected populations.

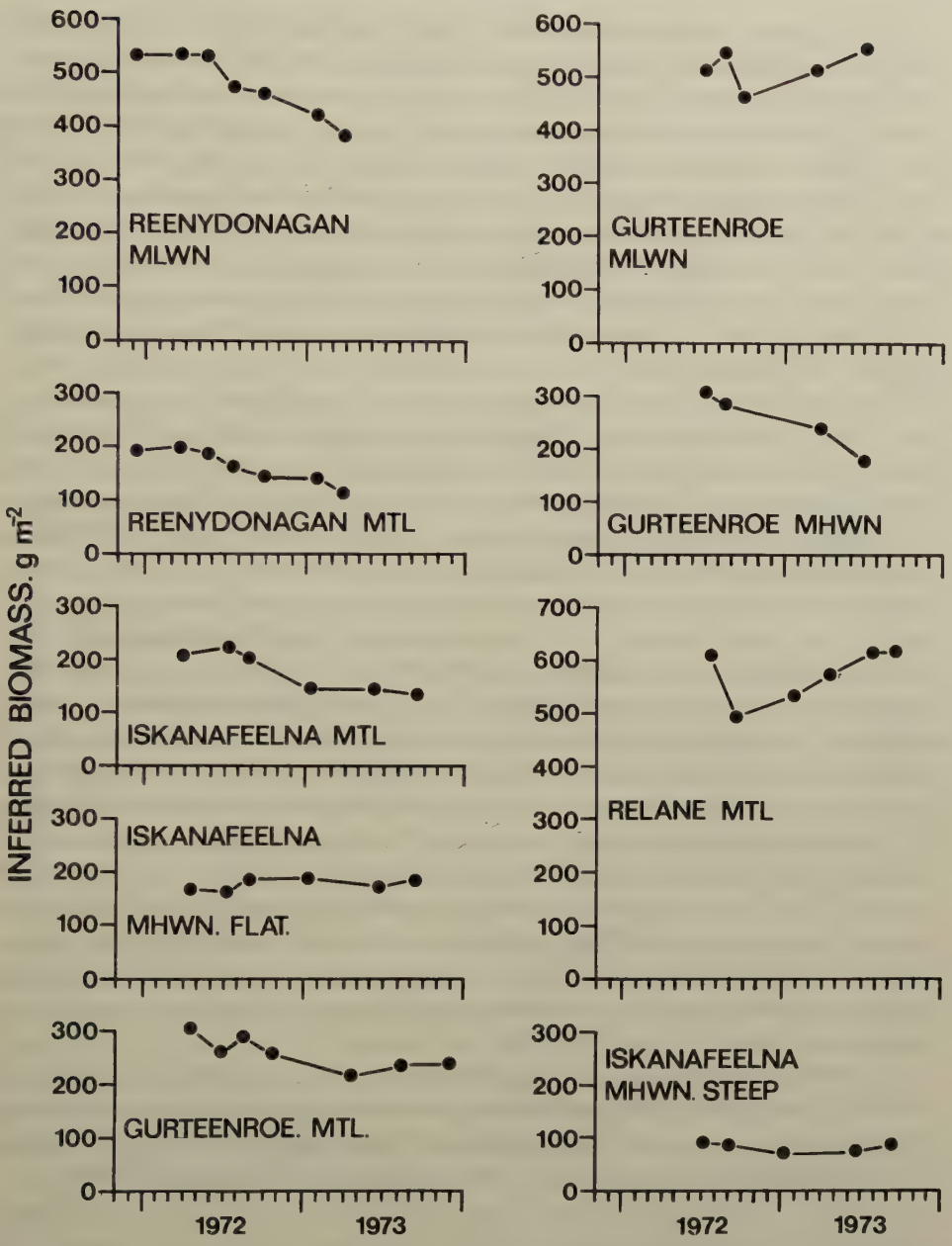

Fig. 15. *Patella vulgata*: changes in inferred biomass in the nine selected populations; biomass was inferred from length-frequency distributions and length-weight curves for each population.

(2) In fast-growing populations, mean lengths by weight were 5–7.4 mm smaller than maximum predicted lengths, except at Iskanafeelna M.T.L. and Reenydonagan M.L.W.N. where they were 18.3 and 0 mm smaller, respectively. These exceptions are in accord with the conclusions reached in (1) above. In the other fast-growing populations the mean length would be reached in 5–6 yr. (3) In slow-growing populations, mean lengths by weight were 7.4–13.6 mm smaller than maximum predicted lengths and were reached in 8–12 yr, except at Iskanafeelna M.H.W.N. Steep; several more years would be required to approach the maximum length. (4) The results are in general agreement with the conclusion that longevity and growth rate are inversely related, but in two of the nine populations growth rate appeared to be variable, changing with time.

The net loss of limpets from most of the selected populations is summarized in Fig. 15, as changes in biomass. Because weights could not be determined in situ, biomass was inferred from length-frequency distributions and length-weight curves for each population. (Length-weight curves were calculated after weighing the surviving limpets at the end of the period of observation.) A net loss in inferred biomass with time was found at five sites, and little change or a net gain at four others: Iskanafeelna M.H.W.N. Flat and Steep, Gurteenroe M.L.W.N., and Relane M.T.L. Because a net loss in numbers or biomass was not seen in all marked populations, it may be concluded that manipulation and marking of the limpets probably did not contribute to mortality. This conclusion is supported by the observation that the change to fucoid domination at Iskanafeelna, attributed to a decline in limpet grazing, affected a much larger area of shore than the experimental sites and their immediate surroundings. Over periods of one or more years, net losses in numbers of *P. vulgata* have been reported by Lewis (1954), Connell (1961) and Jones *et al.* (1977). Net gains have been reported by Fletcher & Jones (1975) and Bowman & Lewis (1977). The latter authors related these changes to variations in recruitment success from year to year. It appears, therefore, that in the selected populations the net losses recorded may simply be part of long term changes in limpet abundance. This may be compared with a 4-yr decline in numbers of the owl limpet *Lottia gigantea*, described by Stimpson (1973).

The observations made on mobility and homing, which indicate that homing is least developed in low-level wet habitats, and most developed on dry rocks with barnacles, are in accord with the conclusions of other workers (Jones, 1948; Lewis, 1954; Ballantine, 1961b; Cook *et al.*, 1969; cf. Mackay & Underwood, 1977).

DISTRIBUTION AND ABUNDANCE

It is clear that local variations in recruitment success, growth rate, and mortality will interact to produce a diverse pattern of population structures. Early work established that such patterns existed in relation to tidal level, exposure to wave action, and the presence or absence of fucoids and barnacles (Hatton, 1938; Fischer-

Piette, 1941, 1948; Das & Seshappa, 1948; Southward, 1953; Lewis, 1954) but understanding of them was severely limited by the lack of a comprehensive scheme for relating populations one to another. Such a scheme was first produced by Ballantine (1961b) using a matrix with vertical zonation and exposure to wave action as its axes. Ballantine stressed his use of Stephensonian zones as the vertical axis; in the present work strict tidal levels were considered more satisfactory. The relation of zones to tidal levels has been described for the Bantry Bay sites by Crapp (1973). Ballantine surveyed six Pembrokeshire shores, sampling at five to seven tidal levels, and he concluded that *Patella vulgata* attained the greatest biomass and mean length by weight at low levels in shelter, especially along the boundaries of bare rock and fucoids. Biomass and mean length both decreased with increasing tidal level and exposure to wave action. The results of the present survey agree well with the conclusions reached by Ballantine, except that the vertical trends in biomass and mean length by weight are reversed in exposure. There is, however, much variability around the major trends. Variability in numbers is attributed mainly to the seasonal appearance and disappearance of juveniles. In terms of weight, a few large animals may have an influence out of all proportion to their numbers. These two factors have less effect on mean length by weight, but all three are very susceptible to the influence of local variations in biological habitat.

This has been studied by Lewis & Bowman (1975), who constructed a matrix similar to that of Ballantine, using tidal level as the vertical axis but with biological habitat replacing exposure-shelter as the horizontal axis. Although Lewis & Bowman presented convincing evidence for the utility of their matrix, it was not possible to arrange the results of the present survey adequately without taking account of the exposure-shelter gradient. Therefore, a matrix was used with biological habitat as its vertical axis and exposure to wave action as its horizontal axis; this was applied to each of four tidal levels, as shown in Figs. 8, 9 and 10. Setting out the results in this way shows that the major trends in population structure are primarily related to exposure to wave action and to tidal level, but changes in biological habitat can exert considerable modifying influence, as described earlier. For the most part, this accords with expectations based on the study of the nine selected populations, and the results of previous workers.

There is still a surprising amount of variation, however, within single habitat types, and this is not so readily explained. It may be suggested that temporal changes be considered as well. For example, in two of the nine selected populations, there were marked changes during the period of study, as the 1970 year class declined at Gurteenroe M.T.L. and as fucoids invaded the shore at Iskanafeelna M.T.L. There was also a fucoid invasion at Iskanafeelna M.H.W.N. Flat, and a discrepancy between predicted and observed maximum sizes at Reenydonagan M.L.W.N. Reference may also be made to the collections made at Dereenacarrin and Ardnagashel, which showed the importance of fucoid cover (Fig. 11). From these data, it is reasonable to conclude that each population has a distinct biological history

and this will exert a profound effect on the population structure that is observed at any one time.

It is argued above that the exposure-shelter gradient is of more significance in accounting for limpet distributions than would be expected from the conclusions reached by Lewis & Bowman (1975). This same opinion was reached, in respect of Anglesey shores, by Jones *et al.* (1977), and exposure-shelter was also accorded primary significance by Ballantine (1961b). This suggests that the perceived significance of exposure-shelter, as opposed to biological habitat, may well vary from one coastline to another.

COMPETITION BETWEEN *P. ASPERA* AND *P. VULGATA*

With increasing exposure to wave action, *P. vulgata* is progressively replaced by *P. aspera*, especially at low tidal levels. Various mechanisms could account for this. For example, Branch & Marsh (1978) have demonstrated marked differences in tenacity (of adhesion to rocks) between six South African *Patella* spp.; species which occur in areas of strong wave action have sacrificed mobility for tenacity. Some species feed only on specific plants, thus limiting their distribution to that of the appropriate plants (Branch, 1971, 1975b). Such mechanisms seem, however, unlikely in the case of *P. aspera* and *P. vulgata*. *P. vulgata* is capable of withstanding extreme wave shock, both at high levels on Bantry shores, and at all levels on more northerly shores (Ballantine, 1961a), and if there were differences in preferred foods, they were not obvious. Ballantine (1961b) found that in *P. aspera*, mean length by weight increased with increasing shelter (see also Fig. 7), and this led him to conclude that competition with *P. vulgata* was all that prevented *P. aspera* from extending into greater shelter in cold areas, as it does in warmer regions. This argument is reasonable, even though competition has never been directly proved by experimental removal of one species alone; it is here assumed that competition does take place.

The distribution patterns of the two species are shown, in extremely simplified form, in Fig. 16. The results for the two species combined are particularly interesting. It appears that competition may be particularly intense at M.L.W.N. on shores of Grade 4, where total limpet wet weights were about 400 $g \cdot m^{-2}$. By contrast, a marked decrease in total weight of limpets was found at M.T.L. and M.H.W.N. on shores of exposure Grades 3 and 4. This is precisely the habitat occupied by *P. depressa* in southwestern Britain (Southward & Orton, 1954; Ballantine, 1961a, b; Moyse & Nelson-Smith, 1963); the species is absent from Ireland (Southward & Crisp, 1954; Ryland & Nelson-Smith, 1975) and was not found in the present survey. In Pembrokeshire, *P. depressa* rarely exceeds 40% of the total weight of *Patella* (Ballantine, 1961b) and it was anticipated that *P. vulgata* would replace it on Irish shores. From Fig. 16, it appears that this may not be so: the niche exploited by *P. depressa* may be unoccupied in its absence. Both *P. aspera* and *P. vulgata* can, however, settle and

survive in this habitat (Fig. 16); the low weights result from a lack of large animals, as reflected in mean lengths by weight (Fig. 7) and length-frequency distributions (Figs. 9 and 10). Perhaps it is significant that *P. depressa* is a small limpet; Ballantine recorded a maximum mean length by weight of 21 mm. It is possible that *P. aspera* and *P. vulgata* do not perform well on mid- to high-level exposed shores while *P. depressa*, an important midshore species in southern Europe (Ballantine, 1961a), may be better adapted to such habitats. It is not a low-shore species, and there was no sag at M.L.W.N.

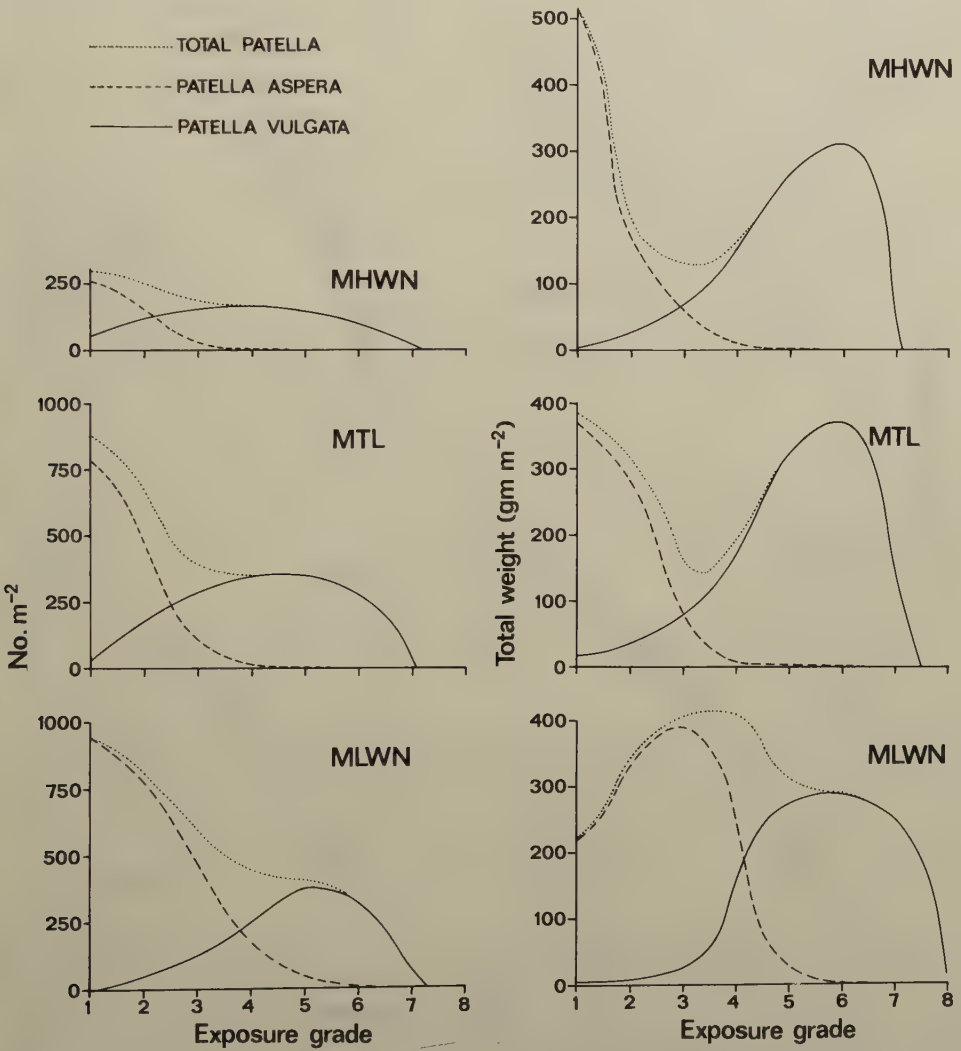

Fig. 16. Major trends in numbers and wet weights · m^{-2} for *Patella aspera* and *P. vulgata* at three tidal levels in Bantry Bay, in relation to exposure to wave action: data for *P. vulgata* are derived from Fig. 6; data for *P. aspera* are from Thompson (1979).

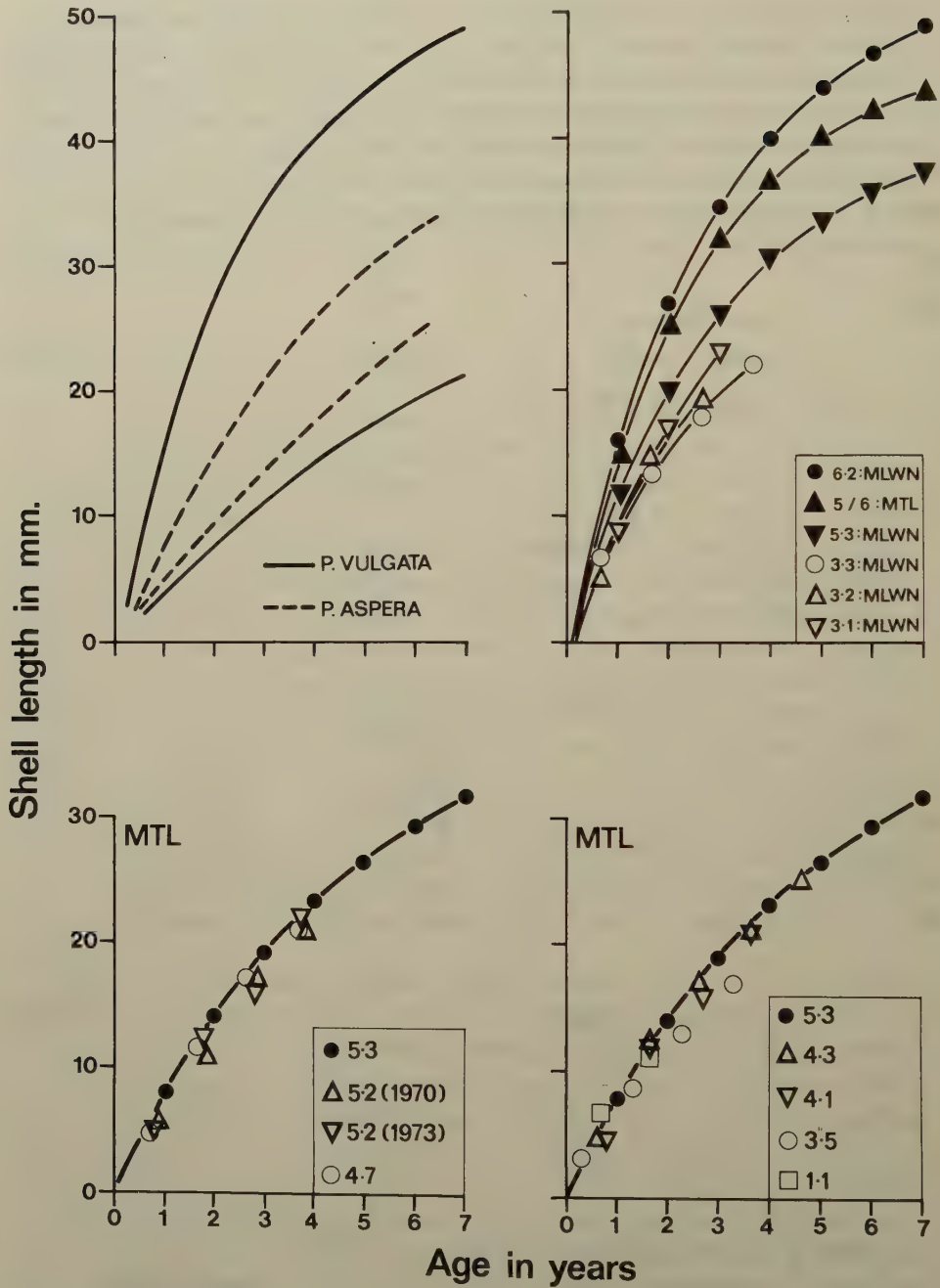

Fig. 17. Growth of *Patella vulgata* from different sites in Bantry Bay. Top left, the range of growth rates reported here for *P. vulgata* is compared to the range found in *P. aspera* by Thompson (1979). Top right, growth curves are shown for wet, low level sites: closed symbols denote results from the selected popula-

Thompson (1979) studied the distribution of *P. aspera* populations in Bantry Bay and concluded that growth rates were slow compared with *P. vulgata* and were also less variable. He predicted that, while the growth rate of *P. aspera* changed very little from one habitat to another, the growth rate of *P. vulgata* should decrease with increasing wave action, probably intersecting that of *P. aspera* at M.L.W.N. on Grade 4 shores. Because few *P. vulgata* survive longer than 2 yr in wet, low-level habitats, most populations are not amenable to length-frequency analysis and it is difficult to obtain sufficient data to test this prediction. All the results that are available are shown in Fig. 17 and from these, it does seem that the prediction is correct for wet, low-level habitats. At M.L.W.N. on Grade 3 shores (there were no results from Grade 4), the growth rate of *P. vulgata* was similar to that of *P. aspera*. In greater shelter, *P. vulgata* grew faster and it might outcompete *P. aspera*.

By contrast, the prediction was not correct in drier, mid-level habitats. Growth rates for M.T.L. mussel, or barnacle and mussel, habitats are also shown in Fig. 17; they are all similar and resemble those found in low-level *P. vulgata* in exposure, or in *P. aspera*. The increased growth rate in *P. vulgata* may depend upon freedom from dry or barnacle–mussel conditions, in addition to reduced wave action.

When the length-frequency distributions of *P. aspera* and *P. vulgata* are compared for each site, it seems that juvenile *P. vulgata* appear sooner and grow faster than do juvenile *P. aspera*, despite earlier spawning in *P. aspera*. *P. aspera* juveniles tend to survive longer, however, at least in habitats supporting adult *P. aspera*. In the examples shown in Fig. 18, the most obvious cohorts are those of 3- to 7-month-old *P. vulgata* and 17- to 21-month-old *P. aspera*. The differences between the species may be summarized by calculating relative numbers and lengths in each identifiable year class, and these values are shown, in relation to exposure to wave action, in Fig. 19. The data are usually based upon limpets 4 to 18 months old but in a few populations results are calculated for limpets up to 43 months old. In these, year class mean lengths converge slightly in the older classes and the proportion of *P. aspera* sometimes declines.

Not surprisingly, there is much variation in the results shown in Fig. 19, but distinct trends can be identified and these confirm that the shift to a lower proportion of *P. vulgata* (with increasing exposure) is paralleled by a decrease in the growth rate of *P. vulgata* relative to that of *P. aspera*.

One point that emerges clearly from Figs. 18 and 19 is the critical importance of

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tions at Gurteenroe (Site 6.2: M.L.W.N.), Relane (Sites 5/6: M.T.L.) and Reenydonagan (Site 5.3: M.L.W.N.), derived from Figs. 4 and 12; open symbols denote results estimated by length-frequency analysis for three populations in bare rock and mussel habitats (Sites 3.1, 3.2 and 3.3). At bottom, growth curves are shown for mid-level mussel, or barnacle and mussel, habitats: closed symbols denote results from the selected population at Reenydonagan M.T.L. (Site 5.3), derived from Figs. 5 and 12; open symbols denote results estimated by length-frequency analysis for three populations in barnacle and mussel habitats (Site 5.2 in 1970 and 1973, Site 4.7) and four populations in mussel habitats (Sites 1.1, 3.5, 4.1, and 4.3).

survival and mortality among the juveniles, described earlier but not discussed as yet. The controlling factors have never been identified, except for the first few weeks when initial desiccation and frosts are important. Bowman & Lewis (1977) suggested that desiccation in the summer of the first year might be the critical factor, but this seems unlikely in the populations described here. First, as shown in Fig. 18, large

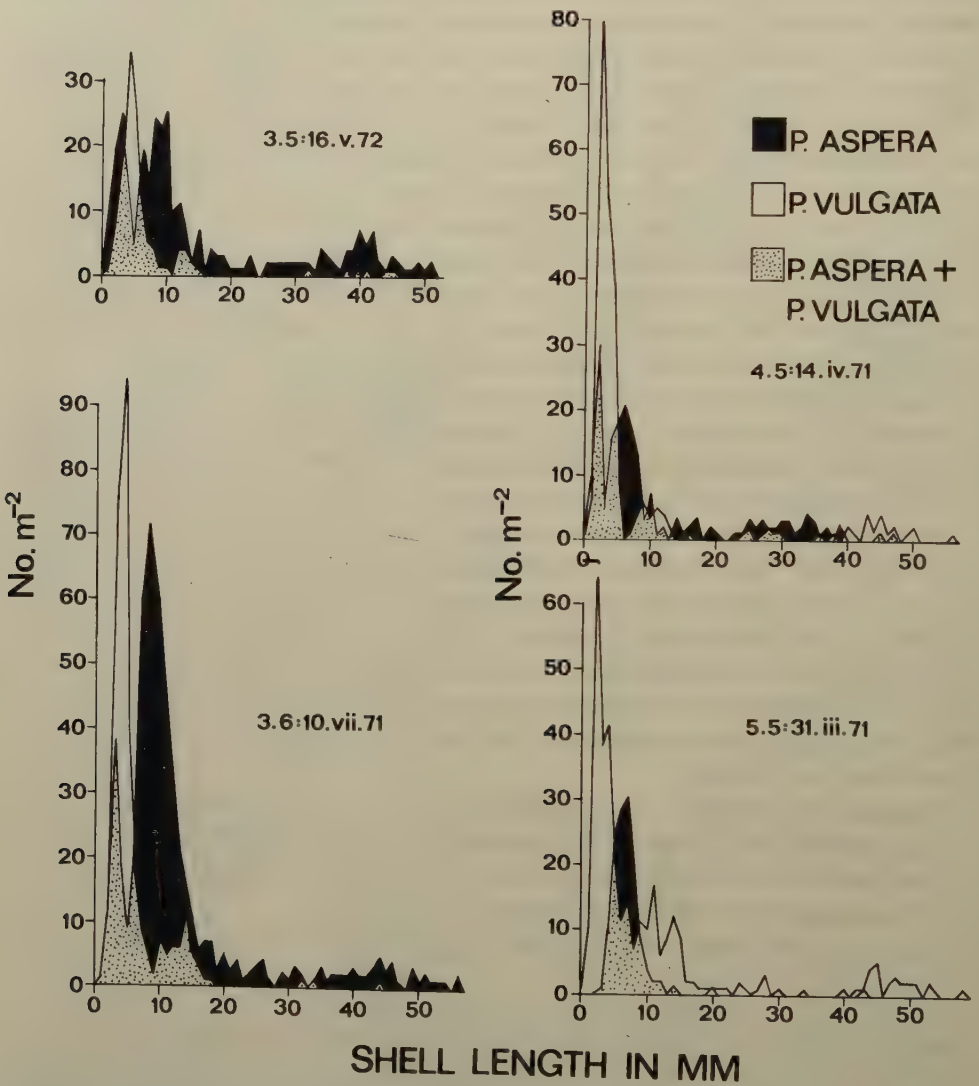

Fig. 18. Length-frequency distributions of *Patella vulgata* compared with those of *P. aspera*, some examples from M.L.W.N., identified by site number and date of collection: in the samples collected in 1971, the most obvious year classes are those for 1971 in *P. vulgata* and for 1970 in *P. aspera*, i.e. the 1971 year class is emerging more slowly in *P. aspera*; a similar pattern was noted, for the equivalent year classes, in other years.

numbers of *P. aspera* juveniles survive for longer than do those of *P. vulgata*. Since *P. aspera* is more susceptible to desiccation than *P. vulgata* (Davies, 1969), it is unlikely that desiccation is important. Secondly, the survival curves shown in Fig. 14 indicate that most mortalities occur in the winter, when desiccation will be least intense.

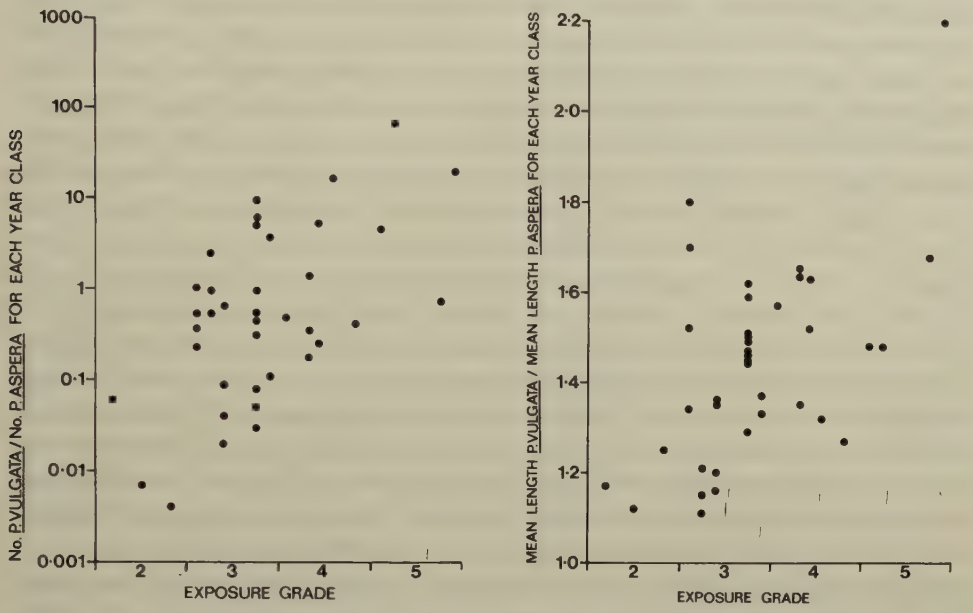

Fig. 19. Relative numbers and relative lengths in *Patella vulgata* and *P. aspera*, in 38 identifiable year classes in samples collected from M.L.W.N.: see text for further details.

Branch (1974b) has shown that in the South African species *P. cochlear* and *P. longicosta*, heavy mortalities occur when the animals change their habitat, moving from the shells that they live on as juveniles, to the rock surfaces or lithothamnia favoured by adults. *P. aspera* and *P. vulgata* do not show such an abrupt transition, but they do change from the damp areas inhabited by juveniles to exposed positions on the open rocks. Ballantine (1961b) described how some *P. vulgata*, living among barnacles at mid- and high-levels, established permanent homes at the end of the second year; he concluded that "this was a dangerous time for the limpet". If juvenile mortalities are the result of a transition from damp juvenile habitats to dry adult homes, this would explain why mortalities occur later in dry areas with barnacles (Fig. 14) and in *P. aspera* (Fig. 18). The transition cannot take place until the animal is able to withstand greater water loss in the new habitat, and this is a function of size (Davies, 1969). It will, therefore, happen later in slow growing animals than in fast growing animals. This hypothesis also accounts for the enhanced survival of juvenile limpets under fucoids (Fig. 14), because the fucoid-bare rock boundary offers a refuge from desiccation that can be exploited by medium-sized

Patella. Thus, it is supposed that desiccation is in fact the direct cause of juvenile mortality, but the limpets encounter it as a consequence of their attempts to move into adult habitats.

Thompson (1979) found that the low shore in extreme exposure could be designated as the centre of the range of *P. aspera*, as defined by Sutherland (1970). The centre of the range for a limpet may be envisaged as that habitat where favourable environmental conditions and reduced interspecific competition permit the species to achieve maximum growth and fecundity. In *P. aspera*, this area was characterized by high densities and low mean lengths by weight, and it may be inferred that the limpets were either short lived or slow growing; the former appeared to be more likely. Moving upshore or into greater shelter, densities were reduced and biomass and mean length by weight increased towards the limits of distribution of the species, at which point there was a rapid decline. Similar distribution patterns have been found in *Acmaea scabra* and *Patella cochlear* by Sutherland (1970) and Branch (1975a). In these cases, the species do not actually attain their full potential in terms of growth and fecundity, because of the existence of severe intraspecific competition.

By contrast, no comparable area which may be designated the centre of the range could be found for *P. vulgata*. The habitat which best approximates this area is that at M.L.W.N. in moderate shelter. Here growth rates are greatest and there is a very high juvenile mortality; thus very few limpets survive to maturity, but those that do exhibit extremely high growth and fecundity. The essential difference between *P. vulgata* and *P. aspera*, therefore, appears to be the difference in juvenile mortality. In *P. aspera*, the unchecked survival of juveniles at the centre of the range may result in severe intraspecific competition. In *P. vulgata*, the recruitment of juveniles into the adult population is restricted; intraspecific competition is, therefore, much reduced and maximum growth and fecundity are realized.

The distribution of *P. aspera* is probably governed by its greater susceptibility to desiccation and its lack of metabolic flexibility (Davies, 1967, 1969; Thompson, 1979). When desiccation and the effects of insolation are reduced, as happens on exposed shores, *P. aspera* is able to outcompete *P. vulgata*, and becomes the dominant limpet species. The better survival of juvenile *P. aspera* could conceivably be a significant factor in this. In greater shelter, *P. aspera* is no longer protected from desiccation at high levels, while at low levels, the more flexible *P. vulgata* grows faster and replaces *P. aspera*. A few *P. aspera* are found at low levels on all shores as far as Grade 6, and might dominate the shore in the absence of *P. vulgata*. At higher levels, *P. aspera* disappears, except on deeply shaded north-facing shores, where desiccation and insolation are much reduced.

Branch (1975b, c) has divided South African *Patella* spp. into "non-migratory" and "migratory" groups, and Thompson (1979) found that *P. aspera* shared many features with the former group. By contrast, *P. vulgata* resembles the species of the migratory group. It is a generalized browser having a random to aggregated distribution. Scars are often poorly defined or temporary, and homing is variable, being

most strongly developed in dry habitats. Upper limits are set by desiccation. There is no marked adult–juvenile differentiation in habitat or food. Selection favours high-replacement populations, showing rapid growth and maturation and large gonads.

The separation of *P. aspera* and *P. vulgata* to the two groups is not well developed, however, and the two species are perhaps more notable for the ways in which the development of "migratory" or "non-migratory" traits varies with habitat as opposed to species. This flexibility is also manifest in the way that the mean length by weight of *P. vulgata* increases in an upshore direction in exposure, and downshore in shelter (cf. Vermeij, 1972). Because there are 11 competing species on the South African shores studied by Branch, and only two species on Irish shores, this lack of specialization is not surprising.

THE CYCLIC RELATIONSHIP BETWEEN LIMPETS AND FUCOIDS

It has long been known that a dynamic relationship exists between limpets and fucoids. Jones (1948) has described "fronts" of limpets moving over the shore and attacking belts of fucoids, while Fischer-Piette (1948) described very dense populations of *P. vulgata* living under stiff sparse fucoids, an exact description of the "dying fucoids" site at Dereenacarrin (Fig. 11 and Table III). Southward (1964) pointed out that the relationship appeared to be cyclic, and that the balance found upon any shore was the result of a temporary stabilization of the cycle at a specific point. In general, shores exposed to wave action tend to become stabilized in favour of the limpets, while sheltered shores are dominated by fucoids.

It has generally been assumed that on an undisturbed shore, the cycle does in fact become stabilized and a definite event is required to re-start it. This is normally the removal of limpets deliberately (Jones, 1948; Lodge, 1948; Burrows & Lodge, 1950; Southward, 1953, 1956; Ballantine, 1961b; Lewis & Bowman, 1975), by scouring (Southward, 1956) or as a result of pollution (Smith, 1968; Crapp, 1971b; Southward & Southward, 1978). The deliberate removal of fucoids normally results in their rapid return, mainly because they are able to re-colonize more rapidly than the limpets (Ballantine, 1961b). Recently, it has been proposed that one or several years of low limpet recruitment can also trigger the cycle (Bowman & Lewis, 1977), and it is clear that low density, low recruitment sites will be most vulnerable to this, especially if it coincides with unusually high adult mortality (Jones *et al.*, 1977).

There is no difficulty in accounting for the sequence of events once fucoids have become established. As pointed out earlier, the establishment of a fucoid cover seems to create particularly favourable conditions for limpet settlement, survival and growth, and a large limpet population may develop and graze down the fucoids that permitted the limpets themselves to appear. This population may be far in excess of that which the shore could otherwise support, and once the fucoids have disappeared, the limpets decline to their normal abundance. This sequence of events

has been described by numerous authors, most recently by Southward & Southward (1978) for shores affected by the Torrey Canyon oil spill. Problems still arise, however, in relation to the initiation of the cycle when starting from limpet domination.

At Iskanafeelna, the events that preceded the fucoid invasion were not obvious or dramatic. At M.T.L. there was a fall in inferred biomass of limpets from 200 $g \cdot m^{-2}$ in August 1972 to < 150 $g \cdot m^{-2}$ in January 1973 (Fig. 15), as a consequence of the disappearance of some of the larger limpets. At lengths of 20–30 mm, 10 out of 23 individuals disappeared, at 30–40 mm, 3 out of 10, and at 40–50 mm, 4 out of 8. At M.H.W.N. Flat, however, there was no fall in inferred biomass, which fluctuated around 180 $g \cdot m^{-2}$, yet fucoids invaded this area as well. It is noteworthy that similar or greater changes were sometimes recorded on other sites (Fig. 15), and an almost identical drop in inferred biomass was seen at Reenydonagan M.T.L. There was no fucoid invasion at the latter site, possibly because around 40% of the rock was covered by small mussels, and so a smaller area was available for settlement of fucoid spores. At Iskanafeelna M.H.W.N. Steep, inferred biomass remained < 100 $g \cdot m^{-2}$ throughout the study, but this site was very different in character, being vertical rock densely covered with barnacles.

Recruitment of limpets in the Iskanafeelna populations seemed to be at a low level but this was considered normal (Fig. 3). Clearly these populations were of the low density, low recruitment type, and a fucoid invasion could easily be triggered by low recruitment combined with high mortality. It may also be that these populations are inherently unstable; hence during limpet–barnacle domination, conditions for limpet settlement and survival may be so severe that too few animals remain to prevent fucoid invasion. The fucoid phase is also unstable, as described above, but the return to limpet–barnacle domination is only made possible by the temporarily favourable conditions (for limpets) found under the fucoids.

It has been recognized that the population balance between limpets, fucoids and barnacles is one that fluctuates with time, but a specific external cause has always been invoked or sought to explain the changes. The argument developed here is itself an extension of the argument that the cycle may be triggered by unusually poor recruitment and survival. In some biological habitats poor recruitment and survival may be usual. The impressive feature of the shores observed in Bantry Bay was the apparent extent of such fluctuations. This was most marked at M.T.L. and M.H.W.N. on exposure Grades 4 and 5. As shores were re-visited, it became apparent that the mosaic of fucoids, limpets and barnacles was constantly shifting. Similar natural fluctuations were described by Burrows & Lodge (1950) and Southward (1956) on the Isle of Man. The population structure of patches within this mosaic was then examined, as at Dereenacarrin and Ardnagashel (Fig. 11 and Table III) and it became clear that the mosaic pattern could not be other than unstable.

This instability does, of course, operate on a very local scale, at the level of patches that are no more than a few m^2 in extent. Although the full cycle from

limpets–barnacles to fucoids may be experienced on each small area, over larger areas of shore the balance between species will tend to be maintained. This was recognized by Southward & Southward (1978), who described the natural balance as either stabilization at a particular point of the cycle, or cyclic changes of a smaller radius. They drew particular attention to the influence of migration on the time scale of the cycle. At one extreme, the cycle can be suppressed by immigration of adult limpets at the beginning of the fucoid phase (Southward, 1956; Aitken, 1962). At the other, the massive mortalities that followed the Torrey Canyon oil spill often eliminated migration as a factor, and cycles of up to 10 years were noted. The influence of other herbivores such as littorinids can have similar effects.

Another mechanism is the effect of a local abundance of *Fucus* spores. This was first noted by Burrows & Lodge (1950), who observed new *Fucus* populations appearing "downstream" of dense growths on an experimental strip. Southward & Southward (1978) were surprised by the extent of some fucoid settlements after the Torrey Canyon oil spill, and commented that local abundance of spores had probably led to more widespread fucoid invasions than would otherwise have occurred. This mechanism is relevant to the present work, since it could account for the appearance of fucoids on the Iskanafeelna M.H.W.N. Flat site, despite the absence of any obvious change in the limpet population. Large patches of *Fucus vesiculosus* occurred within a few metres of the Iskanafeelna sites, and the sporelings that appeared sometimes extended to these patches.

The apparent instability of certain populations must depend upon factors such as the geology of the shore and climate, which influence the settlement and survival of limpets, and which will vary geographically. For example, the patterns observed in Bantry Bay could arise because the rocks there are often smooth, offering young limpets little protection from desiccation unless fucoids or mussels are present. Crapp (1973) found that mussel and fucoid communities were much more important in Bantry Bay than they were in Dale, Pembrokeshire, and stable limpet–barnacle communities are normally found on shores of intermediate exposure in the latter area (Crapp, 1971a). Another possible factor, discussed earlier, is the rôle of *P. depressa*. Bowman & Lewis (1977) suggested that increasing insolation might be the critical factor controlling the southern distribution of *P. vulgata*: "first, by reducing the number of protected microhabitats suitable for initial survival of spat in the autumn, then by increasing greatly the mortality of juveniles during their first spring and summer of shore life, and ultimately by limiting the total population to shaded situations". The instabilities noted in Bantry Bay, and the marked drop in biomass on exposed shores at high levels, may well be the first results of such a trend. In southwestern Britain these results will be less apparent because of the influence of the southern species *P. depressa*.

LIMPET POPULATIONS AS INDICATORS OF CHRONIC OIL POLLUTION DAMAGE

The work described here was designed to provide a means of detecting subtle, long term effects of oil pollution. Recent reviews of such effects (Southward & Southward, 1978) and littoral surveillance (Lewis, 1976) have confirmed the importance of limpets in this respect, but an assessment of the practical value of the survey results is needed.

The original planning of the survey was dominated by the consideration that it was funded for a limited period only. The results, therefore, had to be in a form that could be re-applied at some future date, with no connecting links. In 1970, the expectation was that most changes would be explicable on a tidal level–exposure-shelter matrix, modified by microhabitat changes. To a certain extent this has proved correct, except that the concept of biological habitat has displaced that of microhabitat. The importance of changes in time and local instability was, however, quite unexpected. The implication from this is that population structure depends upon population history, and this can vary greatly between habitats. In retrospect this does not now seem very surprising (cf. Dayton, 1971) but it means that the ability of the survey to detect subtle changes is much less powerful than anticipated. The problem has been discussed in detail by Lewis (1976), and it is apparent that the present work could best be described as pre-surveillance with a monitoring component. Any improvement in its capabilities and accuracy can only come through continued regular surveillance of a limited number of carefully selected sites. Since it is impossible to provide a really satisfactory control site, each stretch of coast having its own unique features, such surveillance should be integrated with similar programmes elsewhere (Bowman & Lewis, 1977; Jones *et al.*, 1977).

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IN SITU SAMPLING OF CRAB BLOOD BY SCUBA DIVERS

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Abstract: Pre- and post-branchial blood samples were taken by SCUBA divers from a natural population of *Cancer pagurus* (L.) and analysed at the site of the dive. The mean P_{O_2} values were 22 and 76, respectively, and there was no significant difference in P_{CO_2} and pH.

Laboratory determinations indicated that air-equilibrated blood had a mean oxygen content of 1.21 mmol O_2/l and a mean protein concentration of 30.6 g/l.

The results are compared with published laboratory investigations which have differed considerably in their description of the blood composition.

INTRODUCTION

Recent investigations into the respiratory physiology of decapod crustaceans have produced differing descriptions of the gas exchange processes. In contrast to the early investigations of Redmond (1955, 1968), Johansen *et al.* (1970) and Taylor *et al.* (1973) have found high oxygen tensions in the post-branchial blood. The values for various species of *Cancer* from these authors are around 100 mm Hg (see Table III). Other investigations have found values of around 40 mm Hg P_{O_2} for post-branchial blood (McMahon *et al.*, 1978) and this has been associated with respiratory pauses lasting several minutes when the heart and scaphognathite activity is reduced (Ansell, 1973; McMahon & Wilkins, 1977). These pauses occur during periods of resting metabolic rate and are less frequent or absent when the crab is excited due to experimental manipulation or spontaneous activity at night (Ansell, 1973).

The oxygen content of the blood has also been found to be very variable in different species of *Cancer* and in different populations of the same species (see Table IV). Although the oxygen content and protein concentration are known to vary through the moulting cycle of crabs (Herbets *et al.*, 1978; Truchot, 1978) some individuals off the west coast of Scotland are apparently without a respiratory pigment (Bottoms, 1978).

In contrast to the variability in blood P_{O_2} and oxygen content, there seems to be general agreement that the post-branchial blood is only slightly more alkaline than the pre-branchial blood (by less than 0.03 pH units) (Johansen *et al.*, 1970; Truchot, 1973; Angersbach & Decker, 1978; McDonald *et al.*, 1979) and that crustacean blood is alkaline to sea water (Howell *et al.*, 1973).

In an attempt to investigate the physiology of *Cancer pagurus* L. in its natural environment we have sampled the blood of a population of crabs by SCUBA divers. We assumed that if the crabs were going through respiratory pauses that could occupy up to 50% of the time (McMahon & Wilkens, 1977) we would obtain some low post-branchial blood P_{O_2} values. Blood samples were taken and analysed for P_{O_2}, P_{CO_2}, and pH on the shore within minutes of their being taken. Total oxygen content (C_{O_2}) of the blood samples and protein content were measured in the laboratory.

Materials and Methods

All the observations were made between 1000 and 1400 at Cove Bay, Aberdeenshire, between April and June 1978. The bay is used continuously by fishermen and at times the rocky bottom is covered with fish waste. The water was turbid in the bay and visibility was limited to around 1 m.

The crabs, *C. pagurus*, were either free-living or had been caught 2 days previously and kept in large creels on the sea bottom. Males and females were used and the crabs measured 10–15 cm across the carapace and weighed from 250 to 500 g. Only crabs that had hard carapaces and that were in the stages C_4 to D_0 of Drach & Tchernigovtzeff (1967) were used.

SCUBA divers took down syringes which had previously been flushed out with sea water so that they contained no air bubbles. The 5-ml Sabre syringes with 40 mm needles contained 0.077 ± 0.004 g of sea water after they were flushed which diluted the 1 ml blood samples. Blood samples were taken from the crabs at ≈ 10 m depth. Practice in the laboratory and care ensured that the samples were taken quickly from previously undisturbed or at least untouched animals. The syringe needle was first inserted under the dorsal surface of the carapace into the area of the heart and about 1 ml of blood withdrawn in not more than 2 min. A second syringe then pierced the sinuses at the bases of the 3rd or 4th pairs of walking legs and a further 1 ml of blood taken. The two labelled syringes were sealed by pushing the needles into rubber bungs and these were then immediately brought to the surface. A small boat was used for transferring the syringes, held in a bucket of sea water at the same temperature as that of the sampling site, from the site of the dive to a mobile laboratory on a pier.

The samples were always measured within 15 min of their being taken and in 12 out of 20 were measured within 5 min. Two measurements were made for each sample of the three measured variables and the mean taken from each replicate.

Samples of sea water were taken from around the crabs at the beginning and end of each dive.

The Radiometer micro-blood gas analyser BMS 3 Mk 2 and a PHM 73 were run at the site on a Honda generator. The water in the water jacket of the Radiometer was circulated through glass coils in a 90-l container of sea water. Ice was added to keep the analyser at the same temperature as that of the sea measured during the first dive of the day with a mercury thermometer.

The Radiometer P_{O_2} electrode (E 5047) was calibrated with air from an air pump and with oxygen-free nitrogen transported to the site in a car inner tube that had previously been evacuated and filled with oxygen-free nitrogen in the laboratory. This method of storing nitrogen was found to be satisfactory from laboratory experiments. The P_{O_2} was calculated from the barometric pressure measured in the laboratory. Duplicate sea water and blood samples agreed to within 2–5 mm Hg P_{O_2}.

The CO_2 electrode (E 5037) was calibrated with a 2% CO_2 in nitrogen and 1% CO_2 in air, the gas mixtures being produced by Westhoff gas-mixing pumps. Gases from the pumps were used to inflate previously evacuated car inner tubes in the laboratory and these were taken to the dive site. The mixtures were used within 12 h of being made and laboratory experiments showed that there was no detectable change in composition over that time. The blood samples were left in contact with the CO_2 electrode for 5 min before the stabilized readings were taken. We did not have the technique of Cameron (1971) and we recognize that measurement of P_{CO_2} at the low levels recorded is difficult (Cameron, 1971; Reeves, 1977; McDonald *et al.*, 1979) and the results are considered with reservation.

pH was measured with a glass micro-electrode (Radiometer G299A) standardized against standard phosphate buffers (Radiometer S1500 and S1510). The electrode was calibrated immediately before every determination but we have found some indication that consecutive readings from the same blood sample show an increased pH measurement. Consecutive measurements of blood pH agreed, however, to within 0.014 ± 0.0031 pH units. Simultaneous measurements of sea water pH were occasionally made with a large glass electrode (Radiometer G2021) and no significant difference in values were obtained compared with the micro-electrode.

Some blood samples were brought back to the laboratory and placed in tonometers (Tucker, 1967) in a gas phase of moist air and after 30 min the total oxygen content was measured with a Natelson micro-gasometer. The accuracy of the Natelson was determined by repeated measurements on the oxygen content of aerated distilled water. The standard error over nine trials was 0.0724 mmol O_2/l. Corrections were made from blanks and duplicate determinations were carried out on each of the blood samples.

Protein determinations of centrifuged blood samples were carried out by the modified Lowry method (Miller, 1959).

Some experiments were carried out with crabs in the aquarium, in which case the Radiometer was run at the aquarium temperature with a thermostatted water bath.

All results are shown as means ± SE. Student's *t* test was used to test significance of differences between means and the 5% level of significance used.

Results

The period between sampling the blood from the crab and measuring its gaseous composition was not more than 15 min. In order to determine the effects of keeping crab blood in plastic syringes, pre-branchial blood samples were taken from *Cancer* in the aquarium and their composition determined. A first measurement was made within 2 min of sampling and subsequently every hour for 4 h. The samples were kept in the plastic syringes with the attached needle sealed with rubber and were stored in water at the same temperature as the aquarium water.

The results are shown in Table I. There was no significant difference in P_{O_2} between the measurements made immediately after sampling and 4 h later. There was also no significant change in pH over the 4-h period. Samples of sea water kept for the same period also showed no significant change in P_{O_2} or pH.

Table I

Changes in crab blood P_{O_2} and pH with storage in plastic syringes: the samples were taken from crabs at 15 °C and the syringes stored at that temperature in a water bath; means ± SE calculated from eight animals are shown.

	P_{O_2} (mm Hg)	pH
Immediately after sampling	14.8 ± 1.9	7.780 ± 0.030
After 1 h	12.5 ± 1.7	7.687 ± 0.041
After 2 h	11.0 ± 1.2	7.694 ± 0.028
After 4 h	11.1 ± 1.2	7.683 ± 0.032

The sea water brought up from the sea bottom at Cove Bay on the days when blood measurements were made had mean P_{O_2}, P_{CO_2}, and pH values of 154.3 ± 2.2, 0.45 ± 0.12, and 7.531 ± 0.107, respectively. There was no significant difference between the sea water samples taken on the three different days of blood sampling. The temperature of the water by the crabs was 12.2 °C. Dives, made in April, when crab blood was not taken, showed that the water in the bay had a pH value of 7.817 ± 0.133 with the same P_{O_2} and P_{CO_2}. Several samples of sea water taken at the same time in the bay did not have different values.

The results of the blood sampling are shown in Table II. In all the crabs the post-branchial P_{O_2} values are higher than the pre-branchial values. There are no significant differences between the post-branchial samples between the different days on which sampling took place. The distribution of the P_{O_2} values is shown in

TABLE II

Pre- and post-branchial blood samples taken from *Cancer pagurus*.

Date	Crab no.	Pre-branchial P_{O_2} (mm Hg)	Pre-branchial P_{CO_2} (mm Hg)	Pre-branchial pH	Post-branchial P_{O_2} (mm Hg)	Post-branchial P_{CO_2} (mm Hg)	Post-branchial pH
17 May 78	1	19	1.5	7.901	53	0.6	7.890
	2	19	1.7	8.008	62	1.4	7.850
	3	15	1.6	7.808	89	2.2	7.807
	4	11	1.3	7.831	69	1.3	7.887
	5	28	1.6	7.780	56	0.7	7.720
3 June 78	6	20	1.8	7.940	62	1.6	7.970
	7	20	1.7	7.807	93	1.5	7.950
	8	24	1.8	7.479	82	1.2	7.618
	9	20	1.0	7.344	58	1.3	7.707
	10	19	1.0	7.284	85	0.9	7.499
	11	38	1.7	7.760	99	0.9	7.595
	12	22	0.8	7.672	43	0.7	7.855
	13	31	1.1	7.820	95	0.8	7.858
	14	48	1.8	7.797	107	1.7	7.720
	15	26	1.5	7.720	70	1.3	7.878
4 June 78	16	16	0.5	7.779	76	0.2	7.846
	17	15	0.3	7.950	85	0.2	7.953
	18	17	0.4	7.962	62	0.4	7.970
	19	17	0.5	7.935	90	0.5	7.929
	20	14	0.5	7.681	78	0.2	7.805
	$\bar{x}$	22	1.21	7.763	76	0.98	7.815
	SE	1.97	0.12	0.044	3.88	0.13	0.030

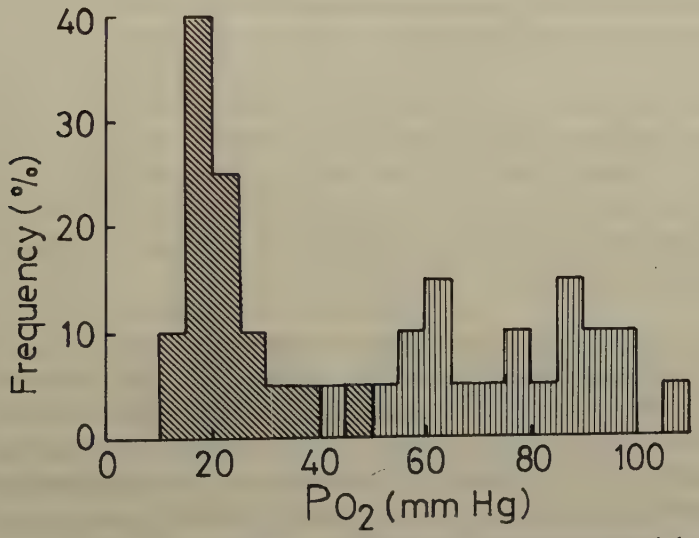

Fig. 1. Distribution of oxygen partial pressures of blood from *Cancer pagurus* sampled on the sea bottom: oblique shading, pre-branchial samples; vertical shading, post-branchial samples.

Fig. 1. The pre-branchial samples mostly fell within a narrow range whereas the post-branchial samples varied considerably.

Although the accuracy of the P_{CO_2} is questionable it is notable that in every case the post-branchial samples had the same or lower P_{CO_2} values than the pre-branchial samples except for crabs numbered 3 and 9. The mean pre- and post-branchial samples are not significantly different but they are significantly higher than the sea-water values.

In Crabs 1, 2, 3, 5, 11, 14, and 19 the pre-branchial blood samples have higher pH values than the post-branchial samples. The means of the pH of pre- and post-branchial blood samples are, however, not significantly different and the means are both significantly higher than the mean sea water pH. The pre-branchial pH values are not significantly different from those of pre-branchial blood from animals in the aquarium (Table I).

The oxygen content of air-equilibrated blood samples was high (see Table IV) and the mean protein content of eight blood samples was 30.6 ± 4.52 g/l.

Discussion

We have found that it is possible for SCUBA divers to take pre- and post-branchial blood samples from crabs on the sea bottom. It remains to be shown whether SCUBA divers taking blood samples from inactive crabs in the sea disturb the animals more or less than blood sampling under laboratory conditions.

Table III

Mean $\pm$ SE P_{O_2} and pH values from pre- and post-branchial blood samples from various crabs: the animals were in water at the temperatures indicated.

Species	Temperature (°C)	Pre-branchial P_{O_2} (mm Hg)	Pre-branchial pH	Post-branchial P_{O_2} (mm Hg)	Post-branchial pH	Reference
Cancer magister (Dana)	8–10	21		91	7.65	Johansen *et al.*, 1970
C. magister	12			40 ± 5	7.84 ± 0.016	McMahon *et al.*, 1978
C. pagurus	12	22 ± 1.97	7.763 ± 0.044	76 ± 3.9	7.815 ± 0.03	Present study
C. productus (Randall)	12	11–20		79–120		McMahon & Wilkens, 1977

Table III shows that the mean post-branchial P_{O_2} value is closer to the high values reported in the literature than to the low values. 25% of the values are >90 mm Hg and 45% >80 mm Hg. Thus, the post-branchial values are not clearly grouped into low values indicative of respiratory pausing or high values indicative of continuous ventilation but the majority of the crabs had values between these two extremes. Certainly the values are not all high in contrast to the results found by

Johansen *et al.* (1970), possibly from excited animals, and by McMahon & Wilkens (1977) for animals not undergoing respiratory pauses.

It is notable that the mean value of the post-branchial Po_2 is close to that found in laboratory experiments with *Carcinus maenas* (L.) when post-branchial blood was taken with a random sampling procedure (81 ± 4 mm Hg, Taylor *et al.*, 1973). These authors suggest that this may be the routine relationship between blood and water oxygen tensions. Our mean post-branchial Po_2 results are also similar to those of Taylor & Butler (1978) for *Carcinus* but much higher than the values for *Homarus* (Butler *et al.*, 1978) and *Astacus* (Angersbach & Decker, 1978).

TABLE IV

Concentration of oxygen (Co_2, total) in *Cancer* blood at post-branchial levels of Po_2 or after air equilibration: the p_{50} are also shown; in the case of the present study $C^{max}_{Hcy}\ O_2$ can be obtained by subtracting 0.195 mmol O_2 from the Co_2 (total), this figure being calculated from the Po_2 and a solubility coefficient (Truchot, 1971); p_{50} taken for pH of blood of around 7.8.

Species	Temperature (°C)	Po_2 (mm Hg)	mmol/l oxygen	p_{50}	Reference
Cancer magister	8–10	91	1.52	19.6	Johansen *et al.*, 1970
C. magister	10			10.2	Wajcman *et al.*, 1977
C. magister	12	90	0.30	7.9	McMahon *et al.*, 1978
C. pagurus	15		0.39	13	Truchot, 1971
C. pagurus	15	150	1.21 ± 0.21		Present study
C. productus	12	112	0.51		McMahon & Wilkens, 1977

Our results with *Cancer* indicate that either individual resting crabs have widely different blood oxygen levels or that each crab is going through cycles of respiration as has been referred to above. Further investigations of animals in situ, whether they be by blood sampling, by heartbeat recordings (Depledge, 1978) or oxygen consumption (Aldrich, 1979) are needed.

In contrast to the post-branchial values, the pre-branchial values are all very similar (Fig. 1). There is some indication that high pre-branchial Po_2 values (Crabs 11, 13, 14) are associated with high post-branchial values. With the mean post-branchial Po_2 values (and even with the lowest value, Crab 12) and the dissociation curves of Johansen *et al.* (1970) and McMahon *et al.* (1978) the blood would be saturated. The pre-branchial blood would be about 55% saturated from Johansen *et al.*'s data and 83% saturated from McMahon *et al.*

The laboratory determinations show that the total oxygen content of the blood sampled from our population was high, almost as high as that recorded by Johansen *et al.* (1970). This is associated with a high protein content of the blood. Truchot (1978) records values between 39.6 and 51.4 protein g/l in the blood of *Carcinus maenas* at stages C_4 and D_0 and $C^{max}_{Hcy}\ O_2$ values of 0.422 to 0.477 mmol/l. These values give a ratio of 101.2 g protein/mmol O_2, whereas from our data for

Cancer the ratio is 30.15 g/mmol O_2. Thus, we have found that *Cancer* blood has a smaller amount of protein per mol of oxygen than *Carcinus* blood. Haemocyanin is the most important protein during intermoult stages in *Carcinus*, comprising 80–90% of the total (Truchot, 1978) and, therefore, the possibility of different oxygen-carrying capacities due to different haemocyanins seems to be likely.

There is no significant difference between the pre- and post-branchial blood in P_{CO_2}. We confirm that the blood is alkaline to the sea water as suggested by Mangum & Shick (1972), Howell *et al.* (1973), and Punzo (1977).

We have found a difference of 0.28 pH units between the sea water at the time of sampling and the post-branchial blood. The OH/H ratio, the relative alkalinity of the blood with respect to neutrality of pure water (Howell *et al.*, 1973) is around 15 from the *Cancer* blood samples which is slightly higher than the value recorded for *Carcinus* by Truchot (1973). Our pH values are very similar to those recorded by others for decapods at similar temperatures (Howell *et al.*, 1973; Truchot, 1973; Butler *et al.*, 1978; Taylor & Butler, 1978). In a number of laboratory investigations a small difference in pH between pre- and post-branchial blood has been found in crustaceans with the post-branchial blood being about 0.03 pH units higher. We have confirmed this observation but found 7 crabs with higher pre-branchial values than post-branchial.

We recorded that the pH was very variable in the small bay and the values could be considerably lower than oceanic sea water (Riley & Chester, 1971). Although interest in acid–base physiology has concentrated on temperature we have found that there can be large local variations in pH at a fairly constant temperature. In addition, crabs brought back from the bay and kept in the aquarium, containing more acidic sea water (pH 7.05), had pre-branchial blood that was not significantly different from that recorded in situ at a sea water pH of 7.53. This would indicate that the crabs are maintaining a constant blood pH at a constant temperature when the pH of the external water may be changing considerably.

It is notable that a number of investigations carried out in situ on the physiology of plants and animals have produced different results from laboratory determinations (Johansen & Vadas, 1967; Miller & Mann, 1973; Houlihan & Newton, 1978; Aldrich, 1979). We also have found that in situ measurements do not accord with some laboratory determinations of blood oxygen tensions.

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EFFECTS OF FOOD AVAILABILITY ON THE VALVE MOVEMENTS AND FEEDING BEHAVIOR OF JUVENILE *CRASSOSTREA VIRGINICA* (Gmelin). I. VALVE MOVEMENTS AND PERIODIC ACTIVITY

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Abstract: The effects of changes in the availability of algal food on the valve movements of juvenile *Crassostrea virginica* (Gmelin) were investigated. Individual oysters were subjected to different conditions: (1) unfed in filtered sea water; (2) continuously fed, in which oysters were given an algal suspension maintained at a constant level (50 000 cells/ml) by an automatic turbidostat; (3) discontinuously fed, where oysters were alternately fed with the turbidostat for 12 h and unfed for 12 h; and (4) batch fed, in which oysters were given specific daily rations at two ration levels (maximum and 40%). Valve movements were concurrently recorded and periods of activity (valves open) and quiescence (valves closed) measured.

Oysters fed continuously remained open an average of 94.3% of the time, whereas unfed oysters were open 35.1% of the time. Discontinuously fed animals were open 95.7% of the time during the times of feeding, but 60.6% of the time during the unfed periods. Activity in the batch-fed oysters was related to the ambient algal concentration in that both the percentage time open/hour and the duration of valve openness decreased with decreasing concentration. Time series analysis of valve movements showed that oysters exhibited a 24-h periodicity of activity when subjected to a 24-h feeding schedule (discontinuous and batch groups) but exhibited no consistent periodicity under the continuous feeding or unfed conditions.

INTRODUCTION

Many species of bivalve molluscs exhibit behavioral periodicity in their valve movements, whereby periods of activity (valves open) alternate with periods of quiescence (valves closed) (Marceau, 1909; Hiscock, 1950; Barnes, 1955; Salanki, 1965, 1966a; Morton, 1969, 1970; Thompson, 1975). During activity the bivalve exposes itself to the ambient environment, ventilates the gills for respiration and food collection, and adducts its valves repeatedly. During quiescence the animal excludes itself from the surrounding conditions, is unable to feed, and generally respires anaerobically.

Periodic activity is affected by physical and chemical factors. A decrease in temperature (Galtsoff, 1928; Hopkins, 1931; Loosanoff, 1939), and O_2 tension (Salanki, 1965, 1966a; Badman, 1974) and either an increase or decrease in salinity (Freeman & Rigler, 1957; Costa & Pritchard, 1978; Djangmah *et al.*, 1979) induce quiescence and cause a general decrease in the total percentage time bivalves are active. Aerial exposure induces closure in some species, depending on the adaptability

of that species to respiration in air (Coleman & Trueman, 1971; Trueman & Lowe, 1971).

Because patterns of activity in bivalves can be influenced by extrinsic factors, numerous studies have focused on the effects of physical parameters on bivalve activity and quiescence and its correlation with diurnal and tidal cycles. Some studies (Morton, J. E., 1956; Morton, B. S., 1971, 1975, 1977; Langton, 1975, 1977; Mathers, 1976) have demonstrated the occurrence of exogenous tidal rhythms of feeding and digestion. Other studies (Loosanoff & Nomejko, 1946; Bennett, 1954; Brown, 1954; Brown *et al.*, 1956; Salanki, 1966b; Morton, B. S., 1969, 1970; Thompson, 1975) have produced conflicting results regarding the existence of endogenous tidal and diurnal rhythms.

The effects of food (organic seston) on the behavior of bivalves have not been directly investigated, however. Previous laboratory-performed studies seldom described the experimental feeding conditions; moreover, animals were often kept in small aquaria without supplemental food. In experiments performed under natural tidal conditions the effects of food availability and of physical factors (e.g., desiccation, temperature), as related to the tide, could not be distinguished. However, Langton & Gabbott (1974), studying the digestive activity of *Ostrea edulis*, subjected this species to a discontinuous (6 h fed/6 h unfed) nontidal feeding schedule, keeping physical factors constant. Under these conditions, digestive tubule structure and crystalline style length were correlated with the schedule of feeding. Considering this, and also Morton's (1973) theory that feeding and digestion in bivalves are discontinuous processes and are interrelated with opening and closure of the valves, it would seem possible that the availability of food, by itself, could affect the duration and temporal pattern of activity and quiescence in bivalves (see Owen, 1974). If this hypothesis is correct, then the results of previous laboratory studies, conducted under artificial or stressed feeding conditions and using valve movements as a criterion for measuring activity, should be interpreted with caution, particularly in regard to rhythmicity.

During periods of activity bivalves repeatedly adduct their valves (Barnes, 1955). These incomplete, quick adductions are possibly associated with feeding and could function to enhance the flow of water across the gills (Hopkins, 1933; Foster-Smith, 1976) or eject pseudofeces (Nelson, 1924b; Galtsoff, 1964). Nelson (1924a, 1960) noted that *Crassostrea virginica* increased its rate of adduction in high turbidity. Experimentation under differing conditions of food availability could further demonstrate the relation between adduction and seston level and more clearly explain the function of adduction.

The objectives of this study were to (1) determine the effects of the availability of food on the temporal pattern of activity/quiescence and the rate of valve adduction in the juvenile American oyster, *C. virginica* (Gmelin), and (2) investigate the interrelation among food availability, feeding behavior, and valve movements in oysters.

Materials and Methods

EXPERIMENTAL ANIMAL

Juvenile *C. virginica* used in the study were laboratory-reared and were sibling progeny of wild adults from local waters of Delaware Bay. Prior to experimentation, oysters were maintained in the laboratory under a 14 h/10 h light–dark cycle at 22 °C for approximately 3 months. During this time, animals were fed a ration of the unicellular alga, *Isochrysis galbana* Parke, once every day, generally between 0900 and 1200. *I. galbana* was subsequently used as food in all experiments. Average whole wet weight of the oysters used in the experiments was 9.5 ± 3.35 g.

EXPERIMENTAL DESIGN

Experiments were designed to demonstrate the effects of (1) presence/absence of suspended algal food, and (2) decreasing concentration of algal suspension on the behavioral patterns of activity and quiescence in oysters. Individuals of *Crassostrea virginica* were subjected to five different feeding conditions: (1) continuous feeding: oysters kept in algal suspension maintained at constant concentration (50 000 cells/ml) for 24 h/day; (2) unfed: oysters kept in filtered sea water 24 h/day; (3) discontinuous feeding: oysters alternately fed in the same manner as condition (1) for 12 h, after which the algal suspension was carefully removed by siphoning and replaced with filtered sea water for 12 h; (4) batch feeding, maximum ration: oysters fed a weight-specific daily ration of algae determined by the formula R (cells/day) = $2.0 \times 10^8 \ W^{0.67}$ (W = whole wet weight in grams) (Epifanio & Ewart, 1977). This ration averaged $9.4 \pm 1.62 \times 10^8$ cells/day. Oysters were fed the same time each day (1000), and aquaria were drained and refilled at the time of feeding to remove any uncleared algae. The algal suspension was grazed for the following 24 h; thus the concentration of suspension was not constant, but decreased with time. Initial algal density was always adjusted to 200 000 cells/ml; (5) batch feeding, 40% ration: oysters fed in the same manner as those in condition (4), except that they were given 40% of the calculated maximum ration (average $3.5 \pm 0.49 \times 10^8$ cells/day). Initial concentration of suspension was adjusted to 80 000 cells/ml.

All experiments were conducted with individual animals in 5-l glass aquaria. A total of five oysters was tested for each feeding regime, as results were reproducible after this number of animals was tested. Different individuals were used for the different feeding conditions, except for the two batch regimes wherein the same five animals were used for both rations. All experiments were conducted in an isolated room in constant low illumination so that oysters would not be exposed to shadows or to general laboratory activity. Water temperature was maintained at 22 ± 2 °C. Salinity was constant at 30‰. Aquaria were continuously aerated with an air pump and stirred with a magnetic stirrer to supply oxygen and prevent settlement of algae. Growth of algae was negligible under these conditions. Water was changed at ir-

regular intervals (20–30 h) for the continuously fed and unfed oysters during experiments. Each animal was allowed to acclimate to light and feeding conditions for 24 to 48 h before measurements of activity were undertaken. Valve movements were recorded continuously for three days following acclimation.

APPARATUS

For the continuous and discontinuous regimes, algal suspension was maintained at constant concentration. This required the continuous monitoring of the *Isochrysis* suspension density and the replenishment of cells removed from suspension by the oyster. An automatic turbidostat (see Winter, 1973) was built for this purpose (Fig. 1).

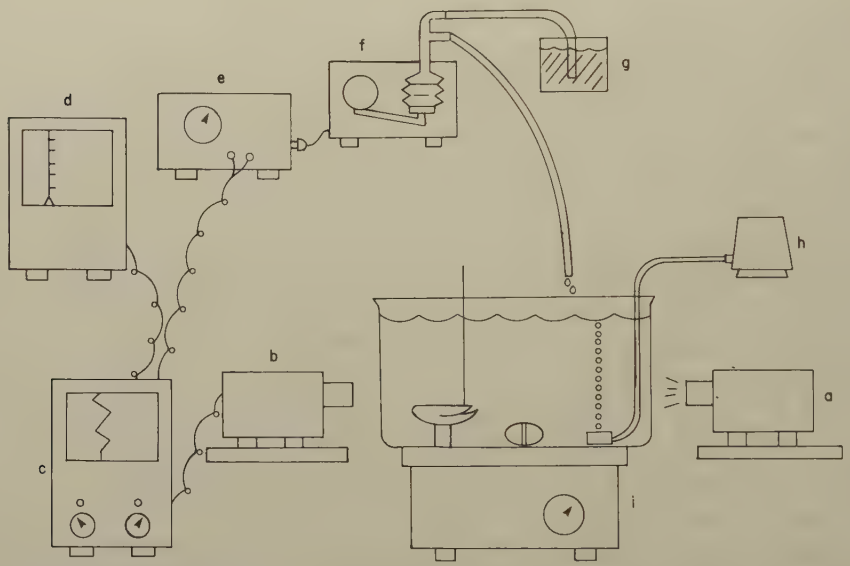

Fig. 1. Apparatus used for maintaining the *Isochrysis galbana* suspension at constant concentration: (a) lamp unit, (b) photocell unit, (c) controller recorder, (d) event recorder, (e) timer unit, (f) bellows pump, (g) reservoir algae, (h) air pump, (i) magnetic stirrer.

A transparent 5-l glass aquarium was used to contain the experimental oyster and algal suspension. Two components of a Radio Shack photoelectric relay system were placed on opposite sides of the aquarium. One component was a light source (high intensity lamp) and the other a photocell/relay unit. For the needs of the experiment the photocell/relay unit was modified by bypassing the relay circuit and utilizing the photocell directly. As a result, the unit could quantitatively detect the amount of light transmitted through the aquarium and thus photometrically monitor the turbidity (density) of the algal suspension.

Output from the photocell was connected to a Rustrak (Gulton Industries, Manchester, N.H., U.S.A.) controller feature recorder (Model 288/F205AB) which con-

tinuously recorded the magnitude of the light transmittance. This recorder contained a threshold feature, such that whenever the electrical input reached a particular high or low threshold, a relay was activated. High or low thresholds could be set to any level with separate dials on the recorder. Preliminary tests were conducted to determine the appropriate level for high threshold, corresponding to the level of turbidity desired for the experiments. As algae were filtered from suspension by the oyster, the transmittance of light through the medium increased; whenever the transmittance attained the preset high threshold level, the recorder relay was automatically activated. Activation of the recorder relay closed a circuit, which turned on a bellows pump. This pumped more algae from a separate reservoir into the experimental suspension. As a result, the turbidity increased and the light transmittance decreased below the threshold level. In addition, the relay of the controller recorder was connected to two other units: (1) an electronic timer (custom made), and (2) an event recorder (Rustrak Model 292). Both units were automatically turned on whenever the threshold relay circuit was closed. The purpose of the timer was to supply voltage to the bellows pump for a specific, constant amount of time. This resulted in the pumping of equal-sized aliquots of reservoir algae into the experimental suspension each time the bellows pump was turned on. The event recorder recorded a mark each time the threshold relay was closed and thus kept a continuous record of the frequency of addition of algae into the experimental medium.

The photocell, lamp unit, controller recorder, and event recorder were AC powered, and their input voltage was regulated with voltage regulators (Sola Electronic, Elk Grove Village, Ill., U.S.A.). The turbidostat was capable of maintaining the concentration of algal suspension constant at 50 000 $\pm$ 5000 cells/ml.

To determine whether the batch-fed oysters cleared the algal suspension over each 24-h feeding period, the concentration of suspension was measured with a Coulter

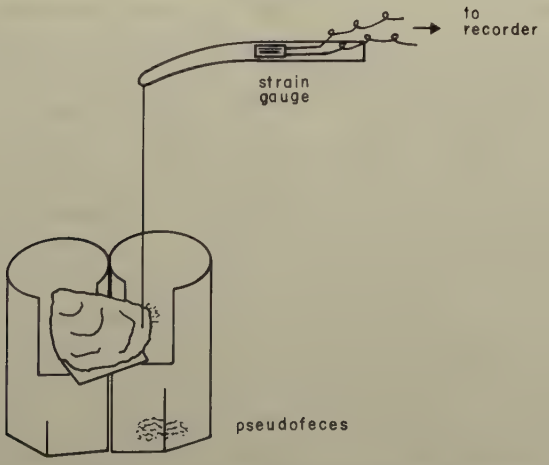

Fig. 2. Strain-gauge apparatus used for the recording of valve movements of the oysters.

counter (Coulter Electronics, Hialeah, Fla., U.S.A.), Model Z_B, fitted with a 70-μm aperture. Counts were made at the beginning ($t = 0$ h) and the end ($t = 24$ h) of each feeding period.

Valve movements of the oysters were recorded using a strain gauge (BLH Electronics, Waltham, Mass., U.S.A.), which was cemented onto a thin, flexible strip of metal that was attached to a nylon line. The line was cemented (with Eastman 910 adhesive) onto the upper valve of the oyster (Fig. 2). Gauge output was recorded by a Rustrak strain gauge recorder (Model 2195). AC input to the recorder was regulated with a Sola Electronics regulator. The strain gauge apparatus was very sensitive to both partial and complete valve movements of the oysters.

ANALYSIS OF DATA

Continuous, 3-day records of valve movements were obtained for each individual oyster. Percentage time open (activity) was determined and averaged for the five animals in each feeding regime. Duration of periods of activity (time between opening and closure) and quiescence (time between closure and opening) were also determined. During periods of activity, the number of quick adductions were counted for each hour and average hourly rates determined.

To determine whether oysters exhibited behavioral periodicity in their valve movements, time series analysis was applied to the data. Records of activity and quiescence for each individual oyster were treated as a time series of integers describing a square wave function (1 = open, 0 = closed). Power spectrum analysis was then performed on the time series using a Burroughs computer program BMD02T (Dixon, 1974). Each time series was shifted time increments of 0.25 h (i.e., 0.25, 0.50, 0.75, 1.0 h ..., etc.) up to a total cumulative shift of 24 h (196 increments). At each shifted time increment, the original time series was correlated with the shifted time series; thus the time series was correlated with itself. Correlation is based on the degree of coincidence of the integers of the original and shifted time series. The magnitude of the power spectrum is a measure of the degree of coincidence of the correlated time series; i.e., the greater the degree of coincidence at a given shifted time increment, the greater the magnitude of the power spectrum. The computer program plots the values of the power spectrum as a function of frequency (1/period = 1/time shifted). Any peaks in the function can be noticed and the period length at which there occurs maximal coincidence of the time series determined. For example, a peak in the power spectrum function at a frequency of $1/x$ h would suggest the existence of a valve-movement periodicity of x h length. The magnitude and isolation of peaks in the power spectrum function are dependent upon the degree of periodic regularity of the time series analyzed. Sharp, isolated peaks of high magnitude are indicative of more overt periodicities than are flat peaks of low magnitude. Thus, qualitative examination of the power spectrum allows consistent, repeatable rhythmic behavior to be distinguished from single, non-repeating events.

Because cultured specimens of *Crassostrea virginica*, which had never been exposed to natural tidal conditions, were used in the experiments, it was assumed that tidal periodicity in these oysters would be nonexistent. Consequently, correlation between valve movements and the local tidal schedule was not examined.

Results

Effects of Presence/Absence of Food on Activity

Typical valve-movement behavior of *C. virginica* under the continuous, unfed, and discontinuous regimes are shown in Fig. 3. Behavior was consistent among all

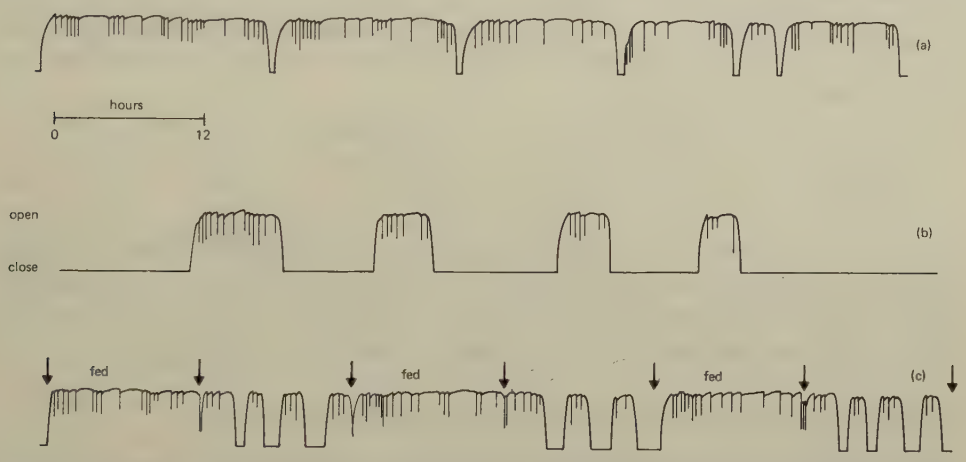

Fig. 3. Representative valve-movements of oysters: (a) fed continuously, (b) unfed, and (c) fed discontinuously; arrows indicate times at which the feeding condition was changed for the discontinuously fed oysters.

individuals within each feeding regime. Average percentage time open and average duration of periods of activity and quiescence for the feeding groups are given in Table I.

Behavior of oysters in the presence of food was strikingly different from behavior during unfed periods. Oysters fed continuously were open almost all the time (average 94.3%), whereas unfed animals were open only 35.1% of the time. However, while no individual under the continuous regime remained open 100% of the time, periods of closure for these oysters were always short, ranging from 0.25 to 1.5 h. Duration of periods of activity for the continuously fed oysters varied considerably (coefficient of variation = 84.1%), ranging in length from 1.0 to 36.5 h. On the other hand, duration of activity in unfed oysters was less variable (c.v. = 46.4%) and shorter, ranging in length from 1.75 to 9.25 h. Periods of quiescence for unfed animals were generally long, ranging in length from 1.75 to 25.25 h.

Oysters under the discontinuous regime exhibited markedly different behavior during times of food presence and absence. In the 12 h that food was present, oysters, like those under the continuous regime, remained open almost all the time (average 95.7%). But in the 12 h when food was absent, time spent open was

TABLE I

Percentage time open and duration of periods of activity and quiescence for oysters under the continuous, unfed, and discontinuous regimes: each figure represents the average ± SE for five individuals; values marked with the same letter are not significantly different (ANOVA, 0.05 probability level).

Feeding regime	% Time open	Average duration activity periods (h)	Average duration quiescence periods (h)
Continuous	94.3 ± 2.35[a]	11.5 ± 9.69[b]	0.6 ± 0.31
Unfed	35.1 ± 5.88	3.7 ± 1.73[c]	7.8 ± 5.85
Discontinuous			
Total	78.9 ± 6.76	3.7 ± 3.82[c]	1.2 ± 1.02
During fed	95.7 ± 6.86[a]	9.9 ± 3.45[b]	1.0 ± 1.33
During unfed	60.6 ± 9.60	1.8 ± 0.72	1.2 ± 1.15

significantly reduced (average 60.6%), and animals underwent frequent openings and closures of short duration. Duration of periods of activity was less variable when considering the fed and unfed subregimes separately (c.v. = 34.9 and 39.6% respectively) than the discontinuous regime as a whole (c.v. = 103.8%).

EFFECTS OF DECREASING CONCENTRATION OF FOOD ON ACTIVITY

In most cases oysters fed under the batch regimes almost totally cleared the *Isochrysis* suspension after 24 h. Final concentrations were usually lower than 10 000 cells/ml and often as low as 2000 cells/ml. On some occasions, however (Oysters 3 and 4, maximum ration, Days 2 and 3), the suspension was not cleared much. It is uncertain why these oysters did not feed on these particular days, but toxic exometabolites produced by senescent algae may have been the cause.

Characteristic valve movements of batch-fed oysters are shown in Fig. 4. Behavior was consistent among most individuals tested and was similar for oysters fed

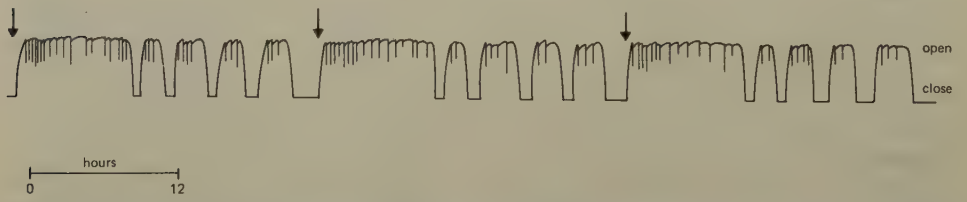

Fig. 4. Representative valve movements of oysters fed under the batch regime: arrows indicate times at which the daily ration of algae was introduced.

the maximum and 40% rations. Percentage time open and duration of periods of activity and quiescence are shown in Table II. Typically, the activity period immediately following the introduction of the algal ration ("first" activity period) was

TABLE II

Percentage time open and duration of periods of activity and quiescence for oysters under the batch regimes: all figures represent the average ±SE for five individuals; values marked with the same letter are not significantly different (ANOVA, 0.05 probability level).

Feeding regime	% Time open	Average duration quiescence periods (h)	Average duration all activity periods (h)	Average duration 1st activity period (h)	Average duration all other activity periods
Maximum ration	74.4 ± 8.94[a]	1.3 ± 1.37	3.9 ± 3.80[c]	9.3 ± 4.05[d]	2.3 ± 1.63[e]
40% ration	66.0 ± 6.52[a]	1.8 ± 1.61	4.0 ± 3.47[c]	8.4 ± 3.18[d]	2.5 ± 1.98[e]

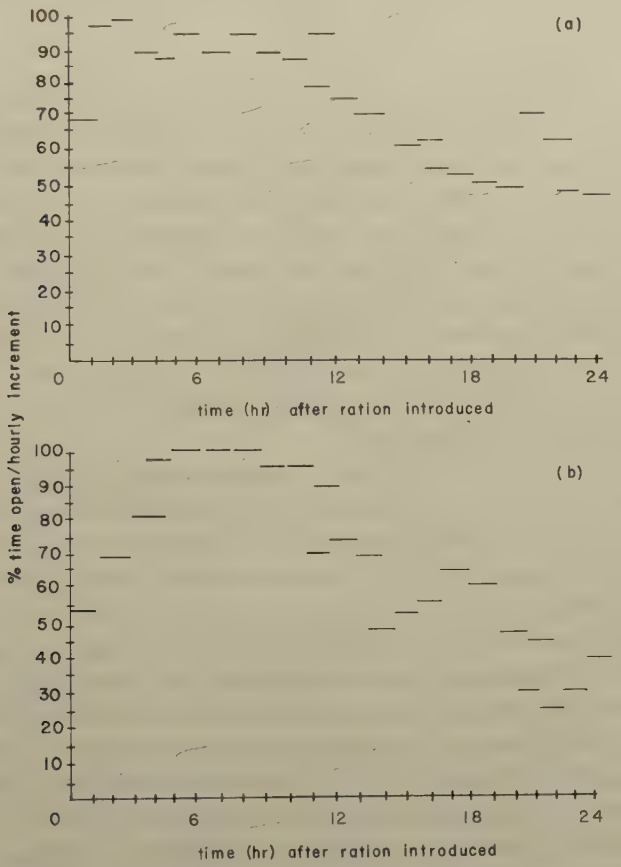

Fig. 5. Average percentage time open/hour (average five animals) for batch-fed oysters given the (a) maximum ration and (b) 40% ration as a function of time after the ration was introduced.

long in duration, and most of the algae cleared within this period. As the concentration of suspension decreased, oysters eventually closed and thereafter began to open and close for short periods. Consequently, variation in the duration of activity periods was great (c.v. = 98.2% for maximum ration, 86.1% for 40% ration). Duration of the first activity period proved to be significantly greater than the average duration of the other activity periods (excluding the first) and was less variable (c.v. = 43.4% for maximum ration, 38.1% for 40% ration). Percentage time open and closed was not significantly different for oysters fed the two different rations.

Duration of periods of activity was related to the ambient concentration of suspension. When algal density was high at the time oysters initiated activity, the duration of the subsequent activity period was greater than when the algal concentration was low at the beginning of activity. Decreasing concentration of suspension also affected activity with respect to percentage time the oysters remained active. As a function of time, average percentage time open/h decreased for both the maximum and 40% ration regimes (Fig. 5).

PERIODICITY ANALYSIS

Results of time series analysis of the valve movements showed marked differences in behavior of oysters maintained under the different feeding regimes. Power spectra often contained multiple peaks, denoting the occurrence of more than one component of periodicity. Many peaks, however, were small or consisted of an indistinct broad peak. These are interpreted as representing either inaccurate or non-overt periodicities. Periods (time shifts) where peaks occurred in the power spectra were determined for each oyster and are presented in Table III. Here, peaks of highest magnitude are distinguished from smaller peaks for each individual. Period lengths represented by broad peaks, estimated by averaging the maximum and minimum values of the peak, are also indicated.

Power spectra for oysters in the continuous and unfed regimes contained many peaks, but few were strong or isolated. Period lengths represented by peaks of highest magnitude, when compared among different individuals, were dissimilar. Periodicity in these oysters, therefore, was inconsistent. In none of these individuals was a 24-h periodicity found.

In contrast, power spectra for oysters in the discontinuous and batch regimes frequently showed highest peaks at a period length of 24 h. Every discontinuously fed oyster and all but three of the batch-fed individuals exhibited a 24-h component of periodicity. Of the batch-fed individuals that did not exhibit a 24-h periodicity, two (Oysters 3 and 4, maximum ration) were the same individuals that did not feed during the course of the experiment. Other components of periodicity, of shorter duration, were present in the discontinuous and batch-fed oysters. In general, these shorter periodicities were less distinct, only a few of which were represented by large peaks in the power spectrum.

TABLE III

Results of power spectral analyses for each individual oyster, all feeding regimes.

Regime, animal nr.	Time shifts (h) at which peaks occurred
Continuous	
1	48.0*; 8.3†; 4.8; 2.9†; 2.0†
2	16.0; 9.6; 6.0*; 4.4; 2.9†; 2.1†
3	14.8*†; 3.3†
4	No peaks
5	12.0*; 6.8; 5.6; 3.8†; 2.5; 2.1†
Unfed	
1	21.3*†
2	13.7*
3	21.3†; 10.6*; 7.4; 5.3; 3.8†
4	14.8†; 7.7*†; 5.2†
5	8.0*†; 4.8*; 4.0
Discontinuous	
1	24.0*; 2.7†
2	24.0*; 3.0†; 2.0
3	24.0*; 6.0; 2.5†
4	24.0*; 3.7
5	24.0*; 3.3†; 2.3†
Batch, maximum	
1	24.0*; 9.6; 3.0†
2	24.0*; 4.0; 2.1
3	16.0*; 6.8; 3.7; 2.5
4	95.0*; 2.9†
5	24.0*; 2.8
Batch, 40%	
1	16.0*; 5.6†; 3.4†; 2.5†
2	24.0*; 4.8†
3	24.0*; 4.0
4	24.0*; 3.1†
5	24.0*; 3.2

* = peak of highest magnitude.
† = peaks represented by bands (flat peak).

RATES OF ADDUCTION

Average rates of adduction during periods of activity for oysters in all feeding regimes are given in Table IV. Adductions/h varied considerably within any given period of activity, regardless of feeding condition. Adduction rate showed no obvious correlation with the availability of food. There was no significant difference in average adduction rate during fed and unfed periods within the discontinuous regime, but oysters in the continuous regime had a higher average rate of adduction than those in the unfed regime. However, unfed oysters had higher rates of adduction than batch-fed oysters, but batch-fed oysters fed the maximum ration had higher rates than those fed the 40% ration.

TABLE IV

Average rates of adduction (adduction/h) by oysters, for all feeding regimes: values marked with the same letter are not significantly different (ANOVA, 0.05 probability level).

Feeding regime	Adduction rate
Continuous	11.4 ± 8.92
Unfed	7.6 ± 4.39^{a}
Discontinuous	
During fed	7.3 ± 3.30^{ab}
During unfed	7.5 ± 5.23^{a}
Batch, maximum	6.7 ± 3.76^{b}
Batch, 40%	4.7 ± 2.62

DISCUSSION

Results of the present experiments indicate that activity in *Crassostrea virginica* is quantitatively affected by the presence of algal food and changes in its concentration. When food is present (continuous, discontinuous, and batch regimes), *C. virginica* is active a significantly greater proportion of the time than when food is absent (unfed regime). Furthermore, as the concentration of food decreases (batch regime), there is an associated decrease in the activity (percent time open) of the oysters.

These results are consistent with those of previous investigations, if experimental conditions are considered. For example, in many cases the experimental animals had been kept in small volumes of water in petri dishes during recording of the valve movements, and undoubtedly any seston would have been quickly removed by the bivalves, depleting the medium of available food. Consequently, percentage time open determined for the bivalves was comparatively low. For example, *Hyridella australis* was found to remain open 53–64% of the time (Hiscock, 1950); *Dreissena polymorpha*, 50% (Morton, B. S., 1969); *Crassostrea virginica*, 40–60% (Brown, 1954); and *Mercenaria mercenaria*, 16–70% (Bennett, 1954). Loosanoff & Nomejko (1946), on the other hand, maintained *Crassostrea virginica* in dockside aquaria into which fresh sea water was constantly pumped. Seston removed by the oysters was thus continually replaced. The greater availability of food under these conditions resulted in the oysters remaining active a comparatively greater proportion of the time (94%).

Many efforts have been made to correlate bivalve activity with diurnal and tidal cycles using data from experiments performed in the laboratory. Hiscock (1950), Salanki (1966b), and Morton, B. S. (1970) found that valve movements exhibited a diurnal rhythmicity in *Hyridella australis*, *Pecten jacobaeus* and *Lithophaga lithophaga*, and *Unio pictorum*, respectively. Also, Bennett (1954), Brown (1954), and Brown *et al.* (1956) claimed that *Crassostrea virginica* and *Mercenaria mercenaria* possessed endogenous diurnal and tidal rhythmicities. However, Brown's (1954)

and Bennett's (1954) results were criticized by Enright (1965) who disproved the existence of these rhythms by reanalyzing the original data. Later, Thompson (1975) recorded valve movements of unfed *M. mercenaria* for up to 16 wk and determined that this species possessed a persistent 24-h periodicity. Gordon (1978), also studying *M. mercenaria* but fed low rations of algae at irregular intervals, could find no diurnal rhythm of valve movements in this species.

Individuals of *Crassostrea virginica* in the present study, when maintained under constant conditions of food presence or absence (continuous and unfed regime), exhibited no 24-h periodicity of activity. Though oysters fed continuously remained open a significantly greater proportion of the time than unfed ones, behavior in both cases was arrhythmic and the initiation of periods of activity and quiescence apparently random. Periodic components found in these oysters were specific to each individual and showed no consistency among different individuals (Table III).

However, oysters subjected to repeated daily feeding schedules (discontinuous and batch regimes) often exhibited 24-h periodicities in activity. Because this behavior was consistent among most individuals and the period length equal to the period length of the feeding schedule, it can be concluded that activity in these oysters was directly influenced by the availability of food. Activity became entrained to exogenous artificial schedules of feeding.

The absence of diurnal periodicity in unfed oysters in the present study is contrary to the results of many investigations previously mentioned. For some, these differences could conceivably be attributed to differences in the experimental light conditions. The present experiments were conducted under constant low illumination, whereas those of Hiscock (1950), Salanki (1966b), Morton (1969), and Thompson (1975) were conducted under either natural or artificial light–dark regimes. Whether the species used in the above studies are photosensitive and modify their valve movements in response to light–dark cycles is uncertain. It is known that *C. virginica* reacts to abrupt changes in light intensity (shadow response). On the other hand, Palmer (pers. comm.) found no effect of light on the pumping rate of this species; thus light may similarly have no effect on long-term valve movements.

Considering the present results and the fact that the bivalve rhythms reported by other investigators were demonstrated under conditions of uncontrolled seston level, it is suggested that the existence of persistent, endogenous diurnal and tidal rhythms of activity in bivalves has not yet been unequivocally proven. Though it is possible that bivalves may possess some degree of endogenous periodicity in their valve-movement behavior, it is uncertain how long this periodicity can be maintained in the absence of varying exogenous stimuli or under the stressful conditions of low food availability.

The reason why oysters, when maintained under the condition of constant food availability (continuous regime), initiate quiescence, and why the duration of valve closure is so short is uncertain. During feeding, the gills could possibly become covered with excess mucus and algal cells, and closure may be required for cleaning

the gill. However, cessation of pumping and/or contractions of the gill muscles could serve this function without necessitating valve closure and consequent isolation from ambient oxygen.

The behavior of *C. virginica* in the discontinuous regime, during the 12-h unfed periods, is similar to the behavior of bivalves under adverse conditions reported by other authors. Galtsoff (1964) found *C. virginica* to alternate short periods of activity and quiescence when affected by poisoning or disease, yet under "normal" conditions (not defined by the author) the valves were open continuously. Badman (1974) showed that *Pleurobema coccineum* remains open continuously when exposed to high O_2 tension, but periodically opens and closes its valves under conditions of low O_2 (feeding conditions were not described in these experiments). Salanki (1965, 1966a) found several species (e.g., *Anodonta cygnea*, *Ostrea edulis*, *Venus verrucosa*) to open and close frequently when the O_2 tension was decreased. Perhaps any condition of stress, whether it is due to changes in O_2, salinity, temperature, turbidity, or nutritive condition, causes bivalves to alternate short periods of activity and quiescence as opposed to remaining open for long periods. During these short activity periods, the bivalves could be testing the medium for suitability. Because the animal is not yet adapted to the altered condition, it closes for a short time to isolate itself from the environment; subsequently, it reopens its valves and reexamines the ambient conditions.

Rates of adduction by *Crassostrea virginica* in this study (Table IV) showed no obvious correlation with the presence or concentration of food, and the present results are difficult to interpret. In some cases, rates of adduction were higher in suspensions of algae than in filtered sea water (e.g., continuous vs. unfed oysters). Conversely, adduction rates were sometimes higher in the absence of algae than in its presence (e.g., unfed vs. batch-fed oysters). Rates of adduction at times were no different in either the presence or absence of algal suspension (e.g., discontinuous during fed vs. discontinuous during unfed). Thus, whether adduction rates in *C. virginica* are affected by seston level and that adduction is involved with the feeding process, cannot be conclusively determined. It is possible that valve adduction rate is dependent on parameters of the individual animal (e.g., size, physiological condition) or is associated with processes other than feeding, such as blood circulation or respiration. If, however, rates of adduction are affected by ambient seston level, as determined by other investigators (Nelson, 1924a, 1960; Loosanoff & Engle, 1947), then the use of adduction rate as a criterion for quantifying bivalve activity (Salanki, 1964, 1966b) when experimental seston levels are not controlled should not be considered valid.

Because none of the feeding conditions in the present study precisely simulate the conditions of food availability in the natural environment, it cannot be said whether or not the behavior of oysters under the continuous, discontinuous, unfed or batch regimes represents natural behavior. It is possible that wild oysters exhibit all of the observed patterns of activity/quiescence, depending on seasonal changes

in the availability of food and the animals' ability to detect these changes and/or endure nutritive stress. In addition, it is not known whether the behavior of juvenile oysters, as determined in this study, is representative of the behavior of adult oysters. Inherent physiological differences between juvenile and adult may bring about differences in the valve-movement behavior.

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DIADEMA AND ITS RELATIONSHIP TO CORAL SPAT MORTALITY: GRAZING, COMPETITION, AND BIOLOGICAL DISTURBANCE[1]

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Abstract: The benthic grazer *Diadema antillarum* Philippi (Echinoidea) has been demonstrated experimentally to contribute to the control of coral community structure in shallow water. In Discovery Bay, Jamaica, West Indies, *Diadema* densities were manipulated over a range of 0–64/m^2 with the aid of enclosures. Grazing by *Diadema* under primary and post-primary succession conditions were compared.

Algal percent-cover decreased as *Diadema* density was increased. Despite the presence of high algal cover, highest coral recruitment and diversity occurred at lowest *Diadema* densities, with planular settlement occurring predominantly in openly exposed micro-habitats. However, since algal growth rates greatly exceeded those of corals, space was rapidly monopolized by the former, resulting in intense competition and high coral mortality. This was particularly evident in *Agaricia* and *Porites* spp. At high *Diadema* densities, coral recruitment was greatly depressed in at least a genus-specific manner by intense levels of biological disturbance resulting from the echinoid's abrasive grazing activities. *Favia fragum* (Esper) was especially susceptible to this perturbation. The surviving coral spat were found generally in cryptic, protected areas. Here they suffered some competitive losses to other sessile epifauna and -flora, particularly coralline algae, polychaetes and forams, which were well adapted to these physical and biological conditions. Increased sedimentation also depressed coral recruitment, replacing grazing as a limiting factor for successful settlement.

Optimal conditions for coral survival, competitive success, and possibly growth were found at intermediate densities due to a balance between competition for space and biological disturbance. *Diadema antillarum* plays an important role in controlling the distribution and abundance of coral spat in the shallow reef community.

INTRODUCTION

Paine's predator removal experiments (1966) demonstrated that the presence of predation could maintain a high species diversity of epifauna in the rocky intertidal zone by decreasing interspecific competition. Later experiments (Paine & Vadas, 1969; Paine, 1971; Dayton, 1973) demonstrated that algae could also be effective competitors for space against epifauna. The absence of predation has been shown to cause local extinction of certain competitively inferior species, and this in turn can cause the disappearance of their associated fauna and subwebs.

Is it possible for an organism associated with, but not included in, a defined

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trophic subweb to be as significantly affected by a predator or grazer as the prey? Evidence suggests this hypothesis in some terrestrial (Laws, 1970; Gorton, 1978) and marine systems. Shallow-water grazers can have a marked effect on sessile invertebrate epifauna (Newman, 1960; Bakus, 1964, 1966; Dayton, 1971). For example, limpets browsing in the intertidal zone can incidentally consume or dislodge newly settled barnacle cyprids (Hatton, 1938; Lewis, J. R., 1954; Connell, 1961; Southward, 1964; Stimson, 1970). This biological disturbance is species-specific in nature and can have just as significant an effect on larval survival as predation has on adults (Dayton, 1971).

The grazer in the study reported here is *Diadema antillarum* Philippi, a common and conspicuous echinoid on Caribbean coral reefs. Coral reefs are renowned for their high diversity and supposed stability (e.g. Sanders, 1969; Slobodkin & Sanders, 1969; Grassle, 1972, 1973; and others). Only recently has *Diadema's* synecology drawn any significant attention (see Ogden *et al.*, 1973a). It is primarily a herbivore (Lewis, J. B., 1964; Atkinson *et al.*, 1973; Ogden *et al.*, 1973a, b, c; Sammarco *et al.*, 1974), although omnivorous activities have been reported for the urchin (Sammarco, 1975, 1977; Bak & Van Eys, 1975; Lawrence & Sammarco, in press).

The algae with which *Diadema* co-occurs are here considered the prey. Their ability to colonize and monopolize space rapidly makes them potentially strong competitors for space (Neill & Larkum, 1966; Sammarco *et al.*, 1974), particularly in the subtidal zone (Vadas, 1968, 1977; Day, 1977). (Specific effects on this group will be discussed in greater detail elsewhere.)

The most important taxon in this study is the "associated group" – the scleractinian corals – a group also dependent on the availability of space for survival and growth. This investigation centers on newly settled coral spat and juvenile colonies, for survival at this stage is crucial to subsequent development of coral community structure (Connell, 1973).

The effects of the grazing activities of *Diadema* on coral community structure, particularly in the early stages of succession, will be considered with respect to coral diversity, abundance, growth, settlement exposure, survival, competitive success, and susceptibility to biological disturbance.

Materials and Methods

STUDY SITE

All experimentation was performed in the shallow lagoon environment at the southern end of Discovery Bay, Jamaica, West Indies (77°24′W; 18°28′N). The experiment was based on Crosby Reef which measures 16 × 60.5 m ($\approx$760 m^2; see Fig. 1), a patch reef heavily grazed by extraordinarily abundant echinoid populations. For example, the average *Diadema* density in fall, 1973 was 71.0/m^2 ($s = 19.45$, $N = 8$). Total echinoid density, including *Echinometra viridis* (A. Agassiz), *Lyte-*

chinus williamsi (Chesher), and *Eucidaris tribuloides* (Lamarck), was 99.5/m^2 (s = 24.79, N = 8). Since all experiments were subtidal, SCUBA was used extensively.

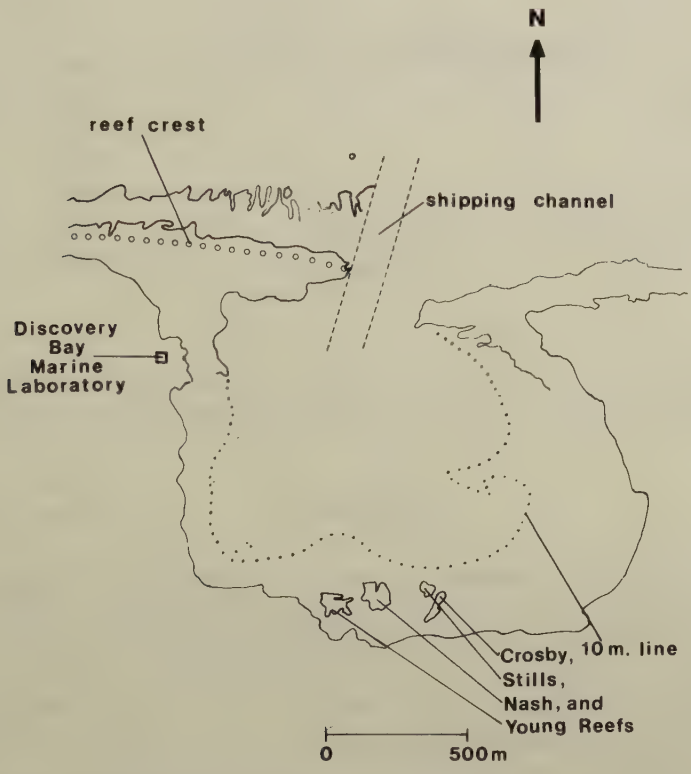

Fig. 1. Map of Discovery Bay, Jamaica, West Indies: Crosby Reef was the study site of this experiment.

EXPERIMENTAL DESIGN

The experiment followed a four-way nested analysis of variance design (see Sokal & Rohlf, 1969). It involved the use of 21 enclosures, 4 m^2 in area (1.82 × 2.19 m) and 0.46 m in height with a mesh-size of 2.54 cm. Each cage was divided in half to separate physically two sub-treatments. The actual placement of the replicate blocks on the reef is shown in Fig. 2.

Four major factors in the experiment were varied as follows.

Diadema density

Experimental densities were maintained at 0, 4, 16 and 64/m^2, falling within the range occurring naturally in the Discovery Bay area. A shortage of time and materials unfortunately prevented use of additional densities. They were randomly

assigned to each cage within a block and maintained by frequent visits and adjustments.

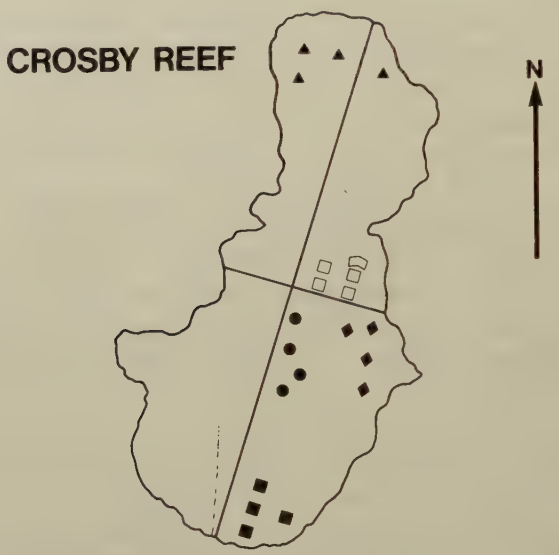

Fig. 2. Location of cages on Crosby Reef: experimental *Diadema* densities within blocks given below, north to south respectively; asterisks indicate cages lost in storms; ●, A-block (4, 0*, 16*, 64/m^2); ■, B-block (0, 64, 4, 16); ▲, C-block (16, 4, 64, 0); ◆, D-block (16, 4*, 0*, 64); □, I-block (16*, 0, 4, 64); ⌓, shading control.

Biological and physical controls (cage design)

Closed-top cages. (1) Winter implantation. These enclosures were implanted in November/December 1973 and included or excluded urchins accordingly while larger fish (e.g., scarids and acanthurids) were excluded. Three replicate blocks were used: the A-, B-, and C-blocks. (2) Summer implantation. One block (D) was implanted 8 months later as a control for seasonal effects.

Open-top cages. Urchins were included or excluded while movements of larger fish were unrestricted. Only one replicate block was used here: the I-block (winter only).

Shading control. This was a sideless structure consisting only of a partition and top, designed to determine the effects of shading. It did not appear to have any effect on the grazing behaviour of local herbivorous fish (winter only).

Stage of succession (substrate)

Primary succession. A natural substratum was used to simulate pioneer conditions – large, flat branches of *Acropora palmata* (Coelenterata : Scleractinia). They were killed in fresh water and introduced into one side of each enclosure. Dead coral tissue was deliberately not removed to promote colonization and substratum preparation by bacteria and blue-green algae.

Post-primary (continuing) succession. The natural surface of the reef within the other half of the cage served as the substratum in this subtreatment – a surface already possessing some portion of the reef community.

Time

Samples were collected twice – once in March and again in October/November 1974. Deterioration of the cages necessitated termination of the experiment at this time.

SAMPLING MODES

Interim samples

The interim samples were small quadrats excised from the reef with the aid of hammer and chisel. These facilitated assessment of coral recruitment rates on a microscopic scale. Three 25-cm^2 samples were initially collected and later increased to six 50-cm^2 quadrats. Samples were selected randomly, sealed separately in labelled plastic bags, and stored by deep-freezing. Later they were thawed and analyzed with a dissecting microscope.

Coral spat as small as 500 μ were identified to genus and often species. Codes for certain species or morphs were assigned to individual colonies where necessary, based on calical structure. Colony size was also estimated by treating the coral as a two-dimensional ellipse with major (maximal longitudinal) and minor (medial) axes. Area was then calculated by the following equation:

$$A = \pi \cdot \frac{\max}{2} \cdot \frac{\text{med}}{2}.$$

Placement of coral settlement of "relative exposure" was also assessed. This acted as an indicator of susceptibility to biological disturbance. Those corals settling on the upper or lateral surfaces of the substrate were differentiated from those settling cryptically on the lower surface.

The "state of well-being" of each colony was also assessed, serving as a general indicator of survival. I designated the "perfect" state as the standard against which all other conditions were judged. The other conditions included a coral (a) being

partially overgrown by a sessile epibiotic associate, (b) exhibiting physical damage to the tissue and skeleton, (c) suffering from both the aforementioned conditions, and (d) exhibiting complete colony mortality. The "condition parameter" was defined simply as the proportion of colonies falling into the "perfect" category. Any significant deviation from normal could then hopefully be detected, irrespective of specific cause.

Any evidence of either intra- or interspecific competition involving corals and other sessile epibiota was recorded (Fig. 3). Associates within 8 mm of the specimen

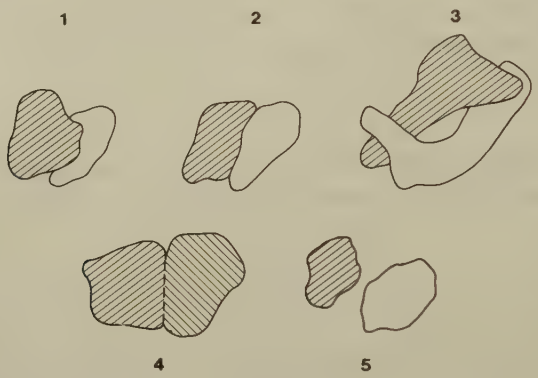

Fig. 3. Competitive processes in coral spat were observed and assessed as follows: 1, coral competitively successful, overgrowing associate; 2, coral competitively unsuccessful, associate overgrowing coral; 3, simultaneous competitive win and loss in different parts of the colony; 4, skeleton and tissue fused between two colonies; 5, no interaction; darkened subject represents coral colony.

were assessed for interaction and recorded. For purposes of this experiment, a static observation of overgrowth was taken as evidence of competition for space (see Jackson & Buss, 1975; Jackson, 1977). Competitive encounters were judged only from the coral's perspective, and the competition parameter was defined simply as the number of competitive wins over the total number of encounters within a taxonomic group. Not knowing a priori which species were better or more important competitors, I weighted all species equally.

Final samples of the primary succession treatment

Upon termination of the experiment, all primary substratum from one experimental block (B-block) was collected and processed. Sample sizes for each treatment were determined through overhead photography and planimetry and standardized to 0.25 m^2. Certain subsamples also received multiple analyses to estimate personal sampling error.

Micro-quadrat samples for percent-cover

Algal percent-cover was estimated with the aid of a 25.4 × 25.4 cm piece of caging mesh subdivided into 100 uniform sample units. Two quadrats were taken per cage per sampling period.

Results

PROBLEMS AND LIMITATIONS

Due to storm activity, a number of cages were lost (0-A, 16-A, 0-D, 4-D and 16-I). In addition, small sample sizes and numbers produced high variances in many cases. These factors made data analyses and interpretation of results difficult in certain instances, particularly in the A-, D- and I-blocks and in the continuing succession treatment. This forced me to rely heavily on the B- and C-blocks for clear, decipherable data. Unfortunately, little can be said here about the effects of seasonality or fish-grazing. (The latter, however, has been investigated through other experimentation and will be discussed elsewhere.)

THE ECHINOIDS AND ALGAE

Attempts to maintain *Diadema* densities close to defined levels and exclude echinoids from experimental areas were generally successful. Total algal percent-

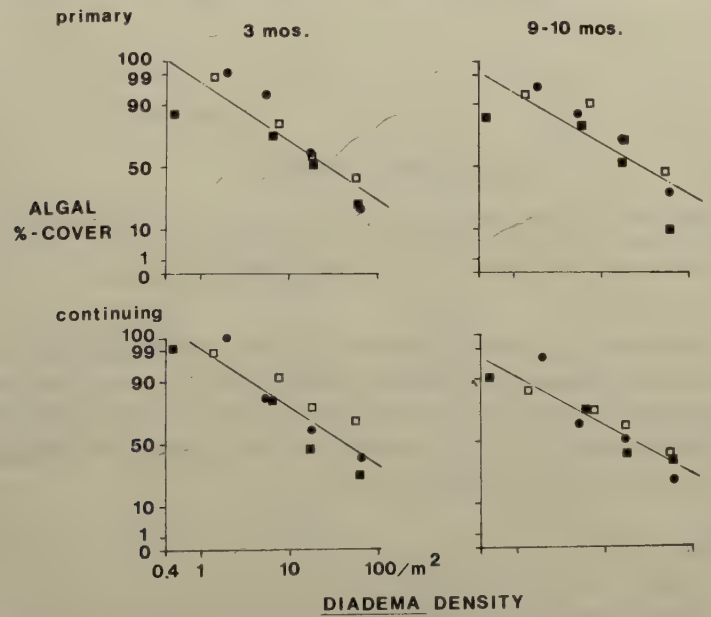

Fig. 4. Percent-cover of algae as a function of *Diadema* density under both primary and post-primary succession conditions: data derived from subdivided quadrats taken at 3- and 9–10 month sampling periods; ●, B-block; ■, C-block; □, I-block; common slopes are shown; all are significant, $P < 0.05$–0.001, analyses of covariance.

cover decreased significantly as *Diadema* density increased (Fig. 4). This relationship was consistent under both primary and post-primary succession conditions and at the 3- and 10-month sampling periods.

THE CORALS (COELENTERATA: SCLERACTINIA)

Diversity

In the primary succession treatment, coral diversity (H'; Pielou, 1969, 1975) was inversely related to *Diadema* density at both the "species" and genus levels (Fig. 5). No significant differences were found with species evenness (J') or number of taxa ($P > 0.05$, two-way ANOVA, linear regression analyses).

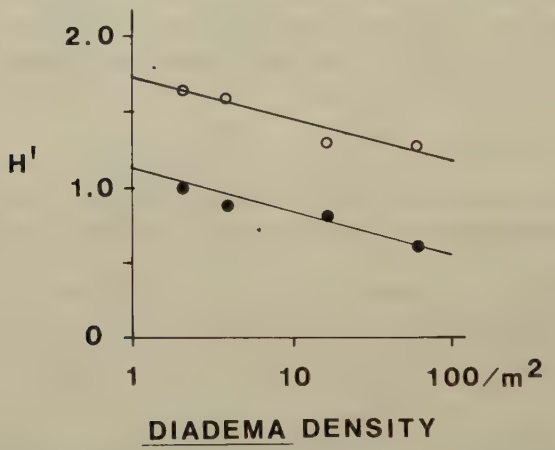

Fig. 5. Coral spat diversity as a function of *Diadema* density under primary succession conditions after 10–11 months: estimated by final samples (B-block); ○, data based on "species"; ●, data based on genera; $P < 0.05$ (species); $P < 0.01$ (genera); linear regression analyses.

Under post-primary succession conditions, diversity did not appear to be related to *Diadema* density except in the open-top cages (I-block). Here, even with a missing replicate, species diversity (H') and generic evenness (J') were inversely proportional to *Diadema* density ($P < 0.01$, linear regression analyses). No discernable pattern of response emerged in number of taxa.

Coral abundance

Primary succession. Increased *Diadema* density clearly depressed success of coral recruitment under primary succession conditions (Fig. 6). Coral colonization was maximal at very low grazing pressures; but even at ≈ 16 *Diadema*/m^2, settlement had fallen to minimal levels.

TABLE I

Coral spat species composition, abundance, and density under varying *Diadema* densities in the primary succession treatment (A): significant decrease noted in total coral density; $P < 0.05$, one-way ANOVA and polynomial regression analysis; *N*, total numbers of corals/treatment; estimates derived from final samples (B-block); relative abundances in percent also shown (B).

A	Experimental *Diadema* density			
Genus species	0	4	16	64
Acropora sp.	2	2	1	
Agaricia agaricites	2	1		
A. fragilis	6	4	3	2
A. 33	26	4		2
A. 34	16		1	
A. (UnID)	90	55	9	9
A. subtotal	140	64	13	12
Favia fragum	84	3		
Helioseris cucullata		3		
Porites astreoides		2		
P. furcata		5		
P. porites		1		
P. 64	24	4		1
P. 65	2			
P. (UnID)	153	72	7	4
P. subtotal	179	84	7	5
N (total)	405	156	21	17
Density (total) in no./0.25 m^2	371.4	90.1	18.6	13.3

B	0	4	16	64
Acropora sp.	0.5	1.3	4.8	0
Agaricia agaricites	0.5	0.6	0	0
A. fragilis	1.5	2.6	14.3	5.9
A. 33	6.4	2.6	0	11.8
A. 34	4.0	0	4.8	0
A. (UnID)	22.2	35.2	42.8	52.9
A. subtotal	34.6	41.0	61.9	70.6
Favia fragum	20.7	1.9	0	0
Helioseris cucullata	0	1.9	0	0
Porites astreoides	0	1.3	0	0
P. furcata	0	3.2	0	0
P. porites	0	6.4	0	0
P. 64	5.0	2.6	0	5.0
P. 65	0.5	0	0	0
P. (UnID)	37.8	46.2	33.3	23.5
P. subtotal	44.2	59.7	33.3	29.4

The larger final samples supported this finding with the total coral density dropping from ≈371 to 13 per 0.25 m^2 (B-block; Table IA). Although *Agaricia*'s density followed this decreasing trend, its relative abundance increased proportionally with *Diadema* density (Fig. 7, Table IB). *Porites*' response was similar to *Agaricia*'s. Although dominant at very low grazing pressures, its density dropped below that of *Agaricia* at high grazing intensities (Fig. 8). *Favia fragum* appeared to be the species most sensitive to grazing. Its density dropped sharply to negligible levels even at four *Diadema*/m^2 and the species disappeared entirely at $\geq 16/m^2$ (Fig. 9).

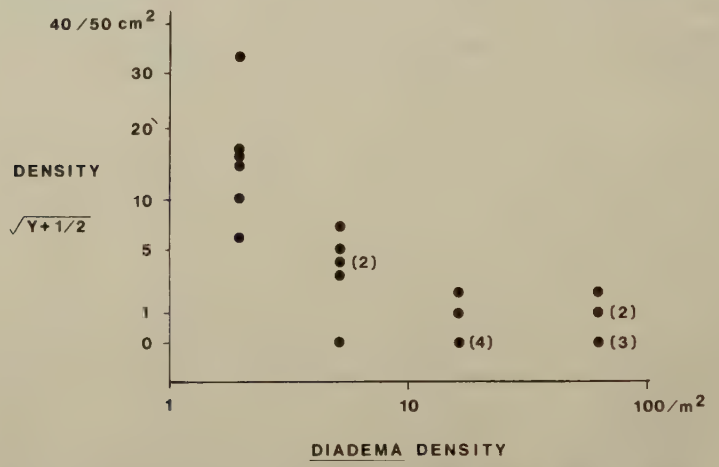

Fig. 6. Density of coral spat as a function of *Diadema* density under primary succession conditions: estimated by interim samples; given in number/50 cm^2 (B-block); multiple points represented in parentheses; $P < 0.01$, one-way ANOVA and polynomial regression analysis.

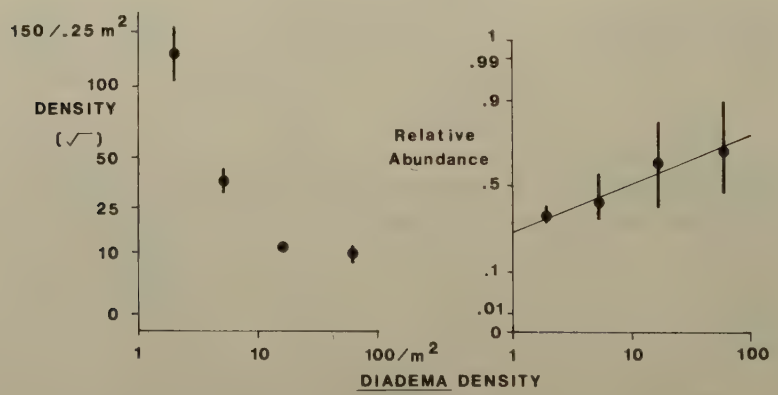

Fig. 7. Density of *Agaricia* spat as a function of *Diadema* density under primary succession conditions with 95% confidence limits ($P < 0.05$, one-way ANOVA and polynomial regression analysis): relative abundance of *Agaricia* in proportions also presented ($P < 0.05$, one-way ANOVA and linear regression analysis); estimates derived from final samples (B-block); $\sqrt{Y}$ and arcsine-Y transformations used respectively for purposes of normalization (see Sokal & Rohlf, 1969, for discussion).

Coral recruitment in the C-block was uniformly low ($P > 0.05$, one-way ANOVA and linear regression analysis). A closer examination of the site and the substratum however, revealed that this block had been implanted in a highly sedimented area.

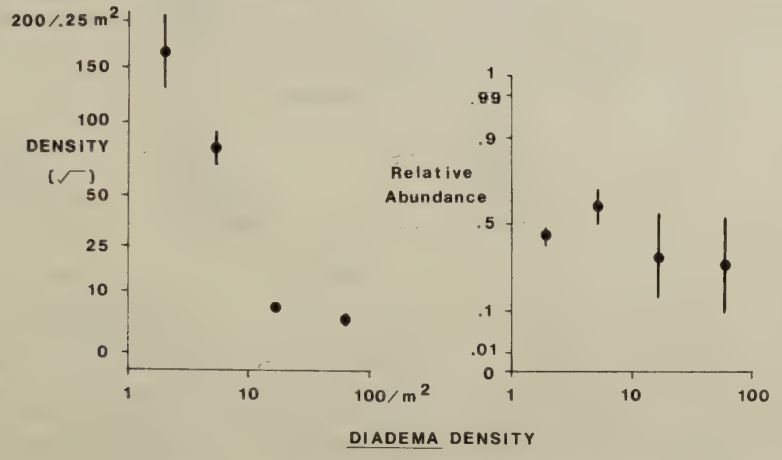

Fig. 8. Density of *Porites* spat as a function of *Diadema* density under primary succession conditions with 95% confidence limits ($P < 0.05$, one-way ANOVA and polynomial regression analysis): relative abundance of *Porites* in proportions also shown.

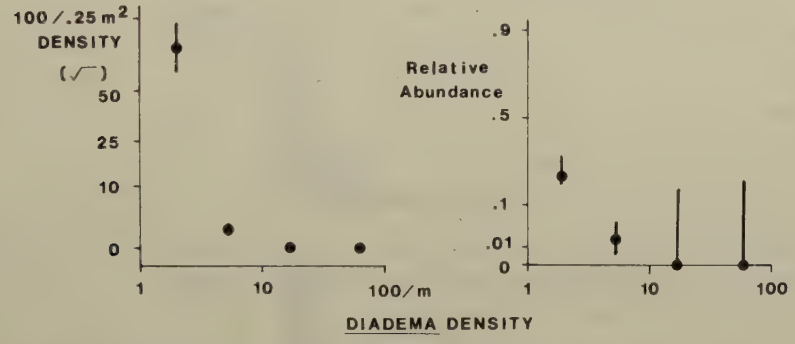

Fig. 9. Density of *Favia fragum* spat as a function of *Diadema* density under primary succession conditions with 95% confidence limits ($P < 0.05$, polynomial regression analysis and one-way ANOVA): relative abundance in proportions also shown.

The open-top cages (I-block) possessed a generally higher level of recruitment than the C-block, but again there were no significant differences between urchin densities.

Continuing succession. The relationship between coral abundance and *Diadema* density was generally less clear here (Table II). For example, coral recruitment followed

TABLE II

Species composition and relative abundances of corals under varying *Diadema* densities in the post-primary succession treatment: *N*, total coral density in number/300 cm^2; blanks represent zeroes, except where density is marked * denoting cage loss; data derived from 10-month interim samples.

Genus species	Cage blocks												
	B				C				I				
	0	4	16	64	0	4	16	64	0	4	16*	64	SH
Acropora cervicornis	1.1		5.9										
A. sp.	3.3	12.5	2.9	9.1	1.8	11.1	3.2	6.1		6.4		3.1	
A. subtotal	4.4	12.5	8.8	9.1	1.8	11.1	3.2	6.1		6.4		3.1	
Agaricia agaricites	1.1		11.8		5.4				6.7	3.2		9.4	11.1
A. fragilis	3.3	12.5	14.7		8.9		3.2	6.1	26.7	19.4		6.2	3.7
A. 33	3.3					5.6	9.7	3.0		3.2		6.2	3.7
A. 34	3.3		2.9		1.2	5.6		6.1	6.7			3.1	
A. UnID	37.7	25.0	38.2	54.5	25.0	22.2	32.2	39.4	26.7	29.0		56.2	51.8
A. subtotal	48.7	37.5	67.6	54.5	40.5	33.4	45.1	54.6	66.8	54.8		81.8	70.3
Favia fragum	2.2	6.2	2.9				12.9			3.2			
Porites astreoides	2.2		5.9				6.4	6.1	6.7	3.2		3.1	3.7
P. porites							6.4						
P. 64	7.7	12.5	5.9	9.1	10.7	27.7	3.2	9.1	6.7	9.7			
P. (UnID)	32.2	25.0	5.9	27.3	39.3	27.7	22.6	21.1	13.3	22.6		9.4	25.9
P. subtotal	42.1	37.5	17.7	36.4	50.0	55.4	38.6	36.4	26.7	35.5		12.5	29.6
Siderastrea radians	1.1	6.25			3.6								
Sp. 80	1.1												
Sp. 130												3.1	
Millepora alcicornis			2.9						6.7				
Millepora sp.					1.2			3.0					
N (no./300 cm^2)	90	16	34	11	56	18	31	33	15	31		32	27

a bimodal pattern in the B-block, with *Agaricia* being primarily responsible for this. The C- and I-blocks again demonstrated no significant pattern.

Coral growth

Although *Agaricia*'s density was highest at minimal grazing pressures under primary succession conditions, 90% of these colonies were ≤ 8 mm^2 in area. Realized colony growth within the experimental *Agaricia* populations was significantly higher at moderate grazing intensities. Due to low coral densities in the 16 and 64/m^2 treatments, no further significant differences could be shown.

Although colonies of *Porites* did not approach the overall sizes attained by *Agaricia*, the mean colony size was again higher at moderate grazing pressures. The size distributions of *Porites* shifted in much the same manner as *Agaricia* (Fig. 10). In *Favia*, the highest mean colony size was attained at lowest *Diadema* densities (Fig. 11).

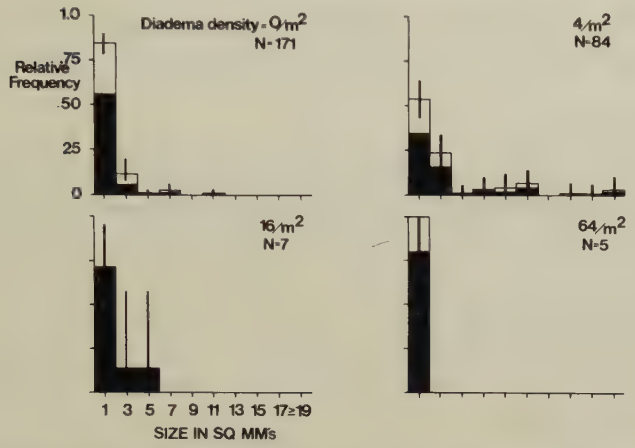

Fig. 10. Relative size frequency distributions of *Porites* under *Diadema* densities of 0, 4, 16, and 64/m^2 respectively in the primary succession treatment: N = total number of colonies/treatment; estimates derived from final samples and given with 95% confidence limits (B-block); colonies under 4 *Diadema*/m^2 treatment significantly larger than those under 0/m^2 ($P < 0.001$, Smirnov's Maximum Deviation Test for Identical Populations; B-block); solid areas represent those colonies in "perfect" condition; maximum height represents the total of all *Porites* colonies, irrespective of condition.

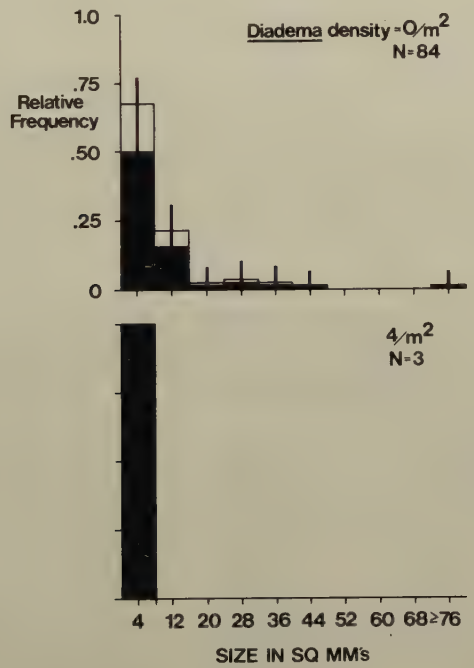

Fig. 11. Relative size–frequency distributions of *Favia fragum* under *Diadema* densities of 0, 4, 16, and 64/m^2 respectively in the primary succession treatment (B-block): N, total number of colonies/treatment; estimates derived from final samples and given with 95% confidence limits.

Due to small sample sizes, no discernable patterns were noted under continuing succession conditions.

Coral settlement exposure

A clear inverse relationship emerged between the degree of exposure in successfully settled corals and *Diadema* density under primary succession conditions (B-

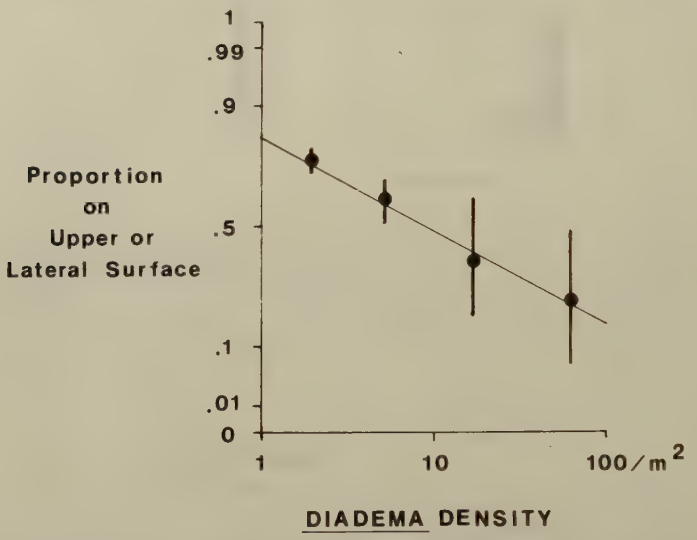

Fig. 12. Relative settlement exposure of coral spat as a function of *Diadema* density under primary succession conditions: exposure index represents the proportion of colonies observed in a fully exposed or lateral position on the substrate; estimates derived from final samples and given with 95% confidence limits (B-block) ($P < 0.01$, linear regression analysis; $P < 0.001$, three-way test of independence).

TABLE III

Relative settlement exposure of coral spat under varying *Diadema* densities in the continuing succession treatment: 1, upper or lateral exposure; 2, cryptic settlement; argument represents number corals/300 cm^2; significant lack of independence found between coral settlement exposure and *Diadema* density ($P < 0.005$, three-way test of independence); estimates derived from 10-month interim samples (C-block).

Experimental *Diadema* Density	Coral genus	Coral exposure 1	2
$0/m^2$	*Agaricia*	15	6
	Porites	22	6
4	*Agaricia*	5	2
	Porites	7	2
16	*Agaricia*	11	4
	Porites	8	4
64	*Agaricia*	5	13
	Porites	6	6

block; Fig. 12). This pattern was well-defined in both *Agaricia* and *Porites*. Under continuing succession conditions, a similar inverse relationship emerged (C-block; Table III).

Coral survival and condition

Coral survival and "state of well-being" were optimized at 16 *Diadema*/m^2 in the B-block under primary succession conditions ($P < 0.05$, two- and three-way tests of independence). This general response was clearer under continuing succession conditions where the proportion of *Agaricia* and *Porites* colonies in "perfect" condition was found to be highest at approximately four *Diadema*/m^2 (C-block; Fig. 13). No significant relationship emerged in the I-block.

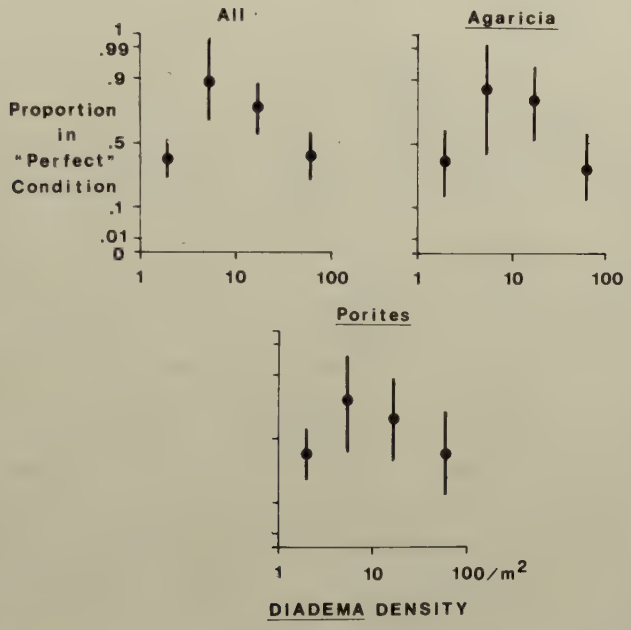

Fig. 13. Condition or "state of well-being" in coral spat as a function of *Diadema* density under post-primary succession conditions for all genera, *Agaricia*, and *Porites*, respectively: condition index represents proportion of colonies observed in a "perfect" state; estimates derived from pooled interim samples and given with 95% confidence limits (C-block); $P < 0.005$, three-way test of independence.

Intra- and interspecific competition

Competitive success in corals was maximized at 16 *Diadema*/m^2 under primary succession conditions, with *Agaricia* making the major contribution to this trend (B-block; $P < 0.001$, three-way test of independence). A similar pattern was noted

TABLE IV

Competition and association matrix for *Agaricia* under varying *Diadema* densities in the primary succession treatment: argument represents total number of competitive wins, losses, or simple associations/0.25 m^2, respectively; 1, competitive win via overgrowth; 2, competitive loss via overgrowth; 5, no interaction; significant peak in competitive success at 16 *Diadema*/m^2 ($P < 0.01$, three-way test of independence); also, significant change in species composition of competitors with increase in *Diadema* density ($P < 0.005$); data derived from final samples (B-block).

Competitor or associate	Experimental *Diadema* density											
	0			4			16			64		
	1	2	5	1	2	5	1	2	5	1	2	5
Corals												
Agaricia spp.	0.9	0.9	11.7			1.2						
Favia fragum			0.9									
Porites spp.			4.6			0.6						
Other epifauna												
Foram 524		0.9										
Foram 525	1.8		1.8									
Foram (UnID)	0.9	1.8	0.9	0.6	0.6							
Gypsina 521 (Foram)	0.9	1.8	0.9	1.2	0.6							
G. 522	1.8	5.5	0.9	1.7		1.2						
Homotrema rubrum	1.8	1.8	8.2	1.7		0.6			0.9			
Haliclona 553 (Porifera)						0.6						
Porifera (UnID)	1.8	1.8	0.9		0.6				0.9			
Spirorbid polychates	19.2	21.1	30.3	5.2	1.7	8.7	4.4		3.5			7.8
Vermetid 570		0.9										
Algae												
Asterocytis ramosa			2.8									
Ceramium sp.						0.6						
Coelothrix irregularis		1.8	3.7									
Corallines, encrusting												
1471	9.2	3.7	3.7	2.3	0.6	2.9				3.1	2.4	0.8
1472	3.7	3.7	1.8	4.6	2.3	2.3				0.8		0.8
1473	0.9											
1475							0.9					
(UnID)		10.1	1.8		0.6							1.6
Cordylecladia peasiae						0.6						
Filamentous chlorophytes	0.9	11.9	36.7	1.7	1.7	8.7			0.9			3.9
Filamentous rhodophytes		2.8	3.7		0.6	2.3						
Gelidium pusillum						0.6						
Herposiphonia secunda			0.9		0.6	5.2						
Lyngbya sp.			0.9								0.8	
Peyssonelia sp.			0.9	0.6								
Polysiphonia sp.		0.9	0.9			0.6						
Total	43.8	71.4		19.6	9.9		5.3	0		3.9	3.2	

under continuing succession conditions, but here *Agaricia* was most successful in competition at an urchin density of $4/m^2$ (C-block; Fig. 14).

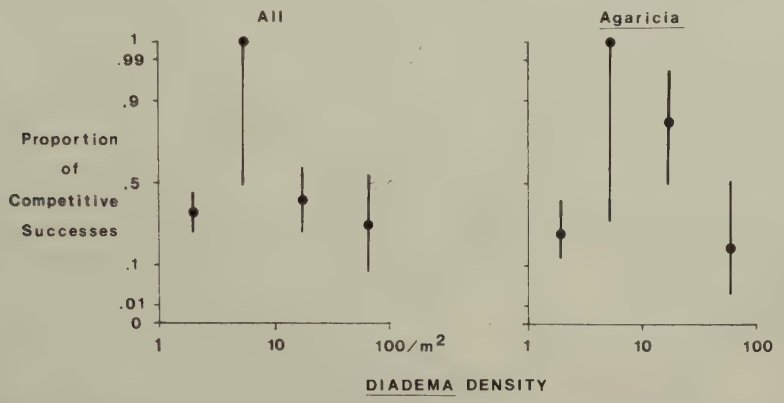

Fig. 14. Competitive success in coral spat as a function of *Diadema* density under post-primary succession conditions for all genera pooled and *Agaricia*, respectively: competition index represents proportion of colonies overgrowing another sessile epibenthic organism if involved in a competitive encounter; estimates derived from pooled interim samples and given with 95% confidence limits (C-block); $P < 0.005$, three-way test of independence.

The major groups found actively competing for space with corals at low grazing pressures under primary succession conditions were foraminifers, filamentous greens, spirorbid polychaetes, and encrusting coralline algae (e.g., Table IV). Under continuing succession conditions, various sponges and red algae were added to the list. But at high *Diadema* densities, the array of competitors changed significantly. Almost all fleshy algae were removed and only corallines and polychaetes remained as important competitors under primary succession conditions. Foraminifers were more important under continuing succession conditions (Fig. 15). Fusion between juvenile corals was rare in this experiment.

Fig. 15. Scanning electron micrograph of an *Acropora* sp. spat (A) simultaneously overgrowing *Homorema rubrum* (Hr) and *Gypsina* sp. (G; Foraminifera): a, overall view (30.5 ×); b, close-up view designating areas of overgrowth with arrows (136.5 ×). ▶

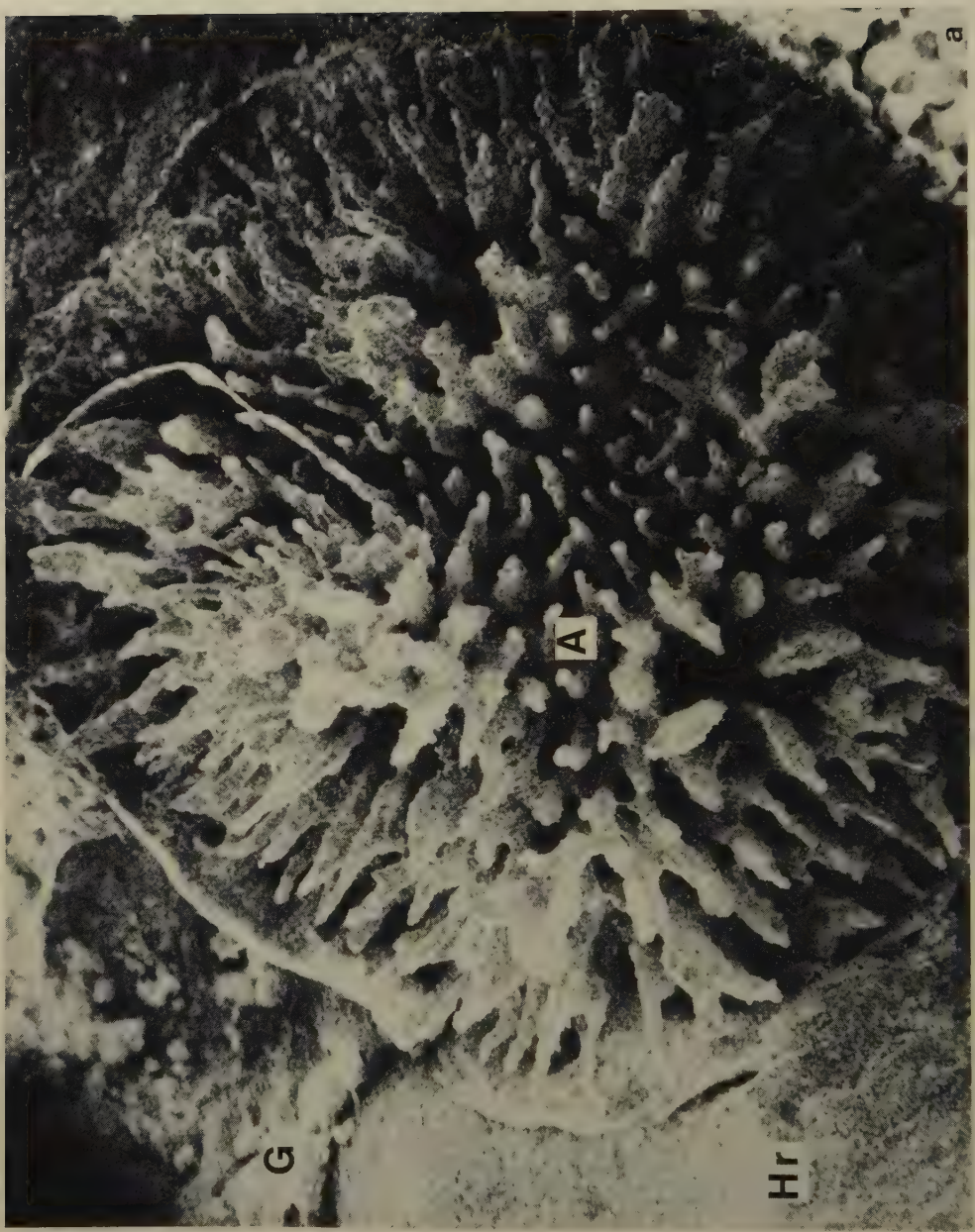

Fig. 15a. For legend see p. 261.

Fig. 15b. For legend see p. 261.

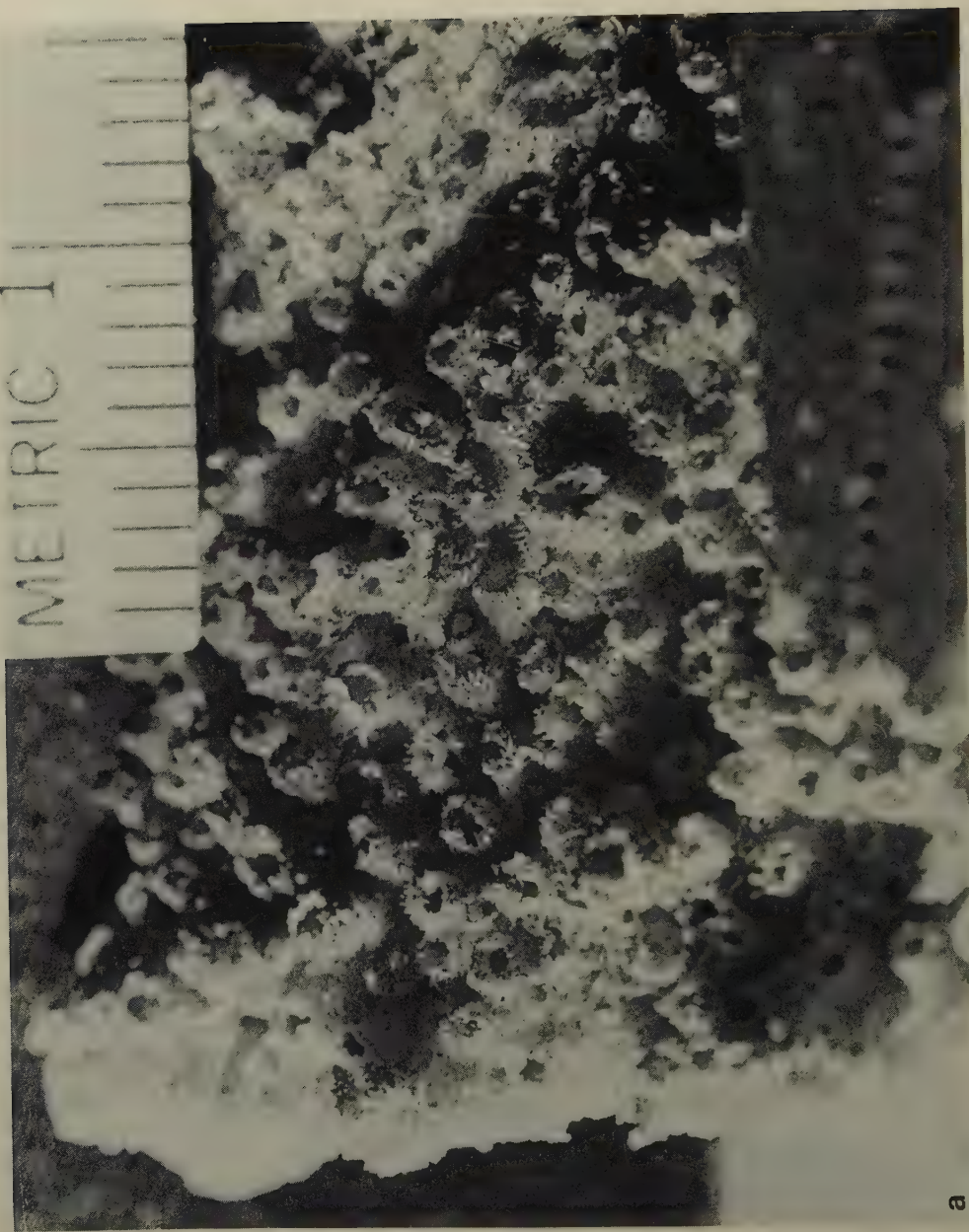

Fig. 16a. For legend see p. 266.

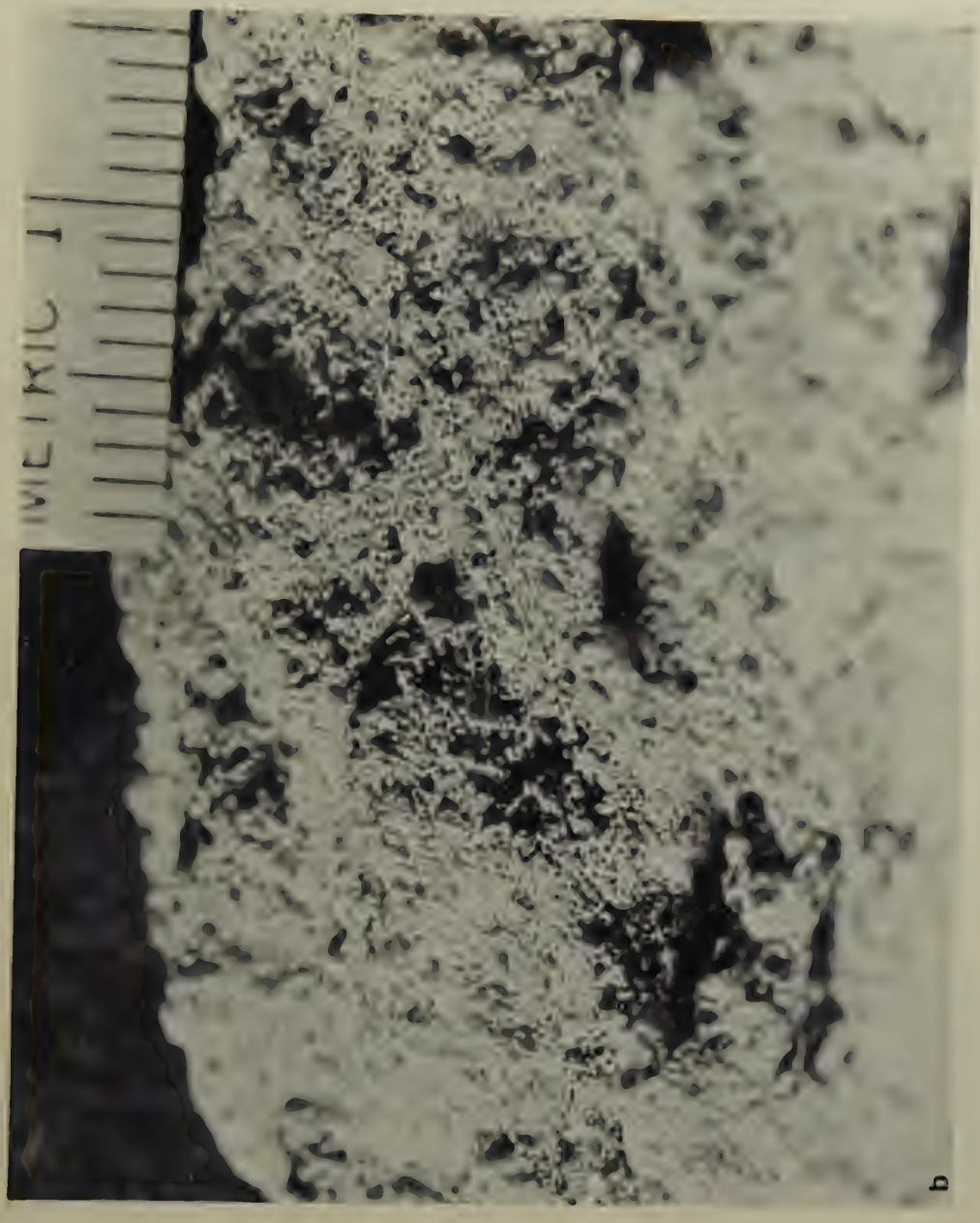

Fig. 16b. For legend see p. 266.

Physical damage; biological disturbance

Under primary succession conditions, little direct evidence of physical damage to coral spat was found. However, the physical micro-structure of the substratum's surface was severely altered. In *Diadema*'s near absence, the surface characteristics were generally well-preserved after a period of 10–11 months, despite severe physical perturbations due to violent storm waves (Fig. 16a). But exposure to 64 *Diadema*/m^2 resulted in the complete destruction of calical integrity, yielding a "sand-blasted" appearance (Fig. 16b).

Direct evidence of biological disturbance was found, however, under continuing succession conditions, particularly in *Agaricia* and *Porites* (A-, B- and C-blocks; Table V). Here recently killed coral spat possessing sheared septa were readily observed at intense grazing pressures (Fig. 17).

TABLE V

Physical damage in coral spat under varying *Diadema* densities in the continuing succession treatment: argument represents number of coral colonies/300 cm^2; significant increase in damage with increased *Diadema* density ($P < 0.005$, three-way test of independence); data derived from 10-month interim samples.

		Experimental *Diadema* density							
		0		4		16		64	
Cage blocks	Coral genus	Grazed	Non-grazed	Grazed	Non-grazed	Grazed	Non-grazed	Grazed	Non-grazed
A	*Agaricia*	–	–	3	39	–	–	5	22
	All	–	–	3	72	–	–	6	34
B	*Agaricia*	1	41	0	5	0	22	1	3
	All	1	86	0	14	4	30	1	9
C	*Agaricia*	0	21	0	7	2	13	2	16
	All	1	53	0	18	5	27	3	31
I	*Agaricia*	1	10	0	13	–	–	2	24
	All	1	15	0	28	–	–	2	31
SH (natural density)	*Agaricia*			1				(2)	(16)
	All							(3)	(24)
Total	*Agaricia*	3	72	3	64	2	35	10	65
	All	3	154	4	132	9	57	12	105

◀ Fig. 16. Microstructure of the upper surfaces of dead *Acropora palmata* branches used as settling substratum in the primary succession treatment: photographs taken after 10–11 months of exposure to 0 and 64 *Diadema*/m^2 (a and b), respectively; scale in mm.

Shading

Shading was found to have no significant effect on any of the variables considered here ($P > 0.05$ in all tests).

Discussion

If competition were the only force governing the distribution and abundance of coral settlement, one would expect, as Dart (1972) has suggested, that as algae are removed with increased grazing pressure, the limiting resource of space would be relinquished for use by corals, and their abundance would increase. This was not the case. Coral recruitment was highest in the absence of grazing or at very low grazing pressures. Corals and algae can and will colonize simultaneously. In this case, biological disturbance prevented successful settlement at higher echinoid densities.

The relationship between coral settlement and echinoid density is essentially negated by high sedimentation. Here grazing or lack thereof is no longer an important limiting factor. Coral planulae probably demonstrate negative settlement preferences for heavily sedimented habitats and/or experience high mortality rates there, as other investigators have also observed or hypothesized (Stephenson, 1928; Stephenson *et al.*, 1958; Yonge, 1963; Loya & Slobodkin, 1971; Mergner, 1971; Pillai, 1971; Porter, 1972).

As mentioned earlier, the effects of fish-grazing on coral recruitment unfortunately cannot be properly evaluated here but will be discussed elsewhere.

The spat of all coral species considered here seem to be sensitive to biological disturbance, but the degree of this sensitivity (or susceptibility) is at least genus-specific. This causes shifts in dominance and relative abundances in corals as grazing pressure varies, contributing to changes in species diversity and evenness. For example, *Porites* replaced *Agaricia* as the dominant species under primary succession conditions when grazing pressure was increased, while *Favia* disappeared entirely from the experimental community at higher urchin densities.

The non-linear response of coral density to *Diadema* density under continuing succession conditions is probably best explained by the nature of the substratum. The natural surface of a reef is much more complex than that of the *A. palmata* substratum used in the primary succession treatment, predominantly as a result of extensive bioerosion from endolithic bivalves, sponges, polychaetes, and other borers. The substratum's heterogeneity provided refuges for coral spat at almost any level

Fig. 17. Scanning electron micrograph of newly settled *Porites* spat: the first specimens (a) were alive and intact when sampled; the second (b) had been freshly killed, showing evidence of sheared septa most likely from echinoid browsing (60 ×). ▶

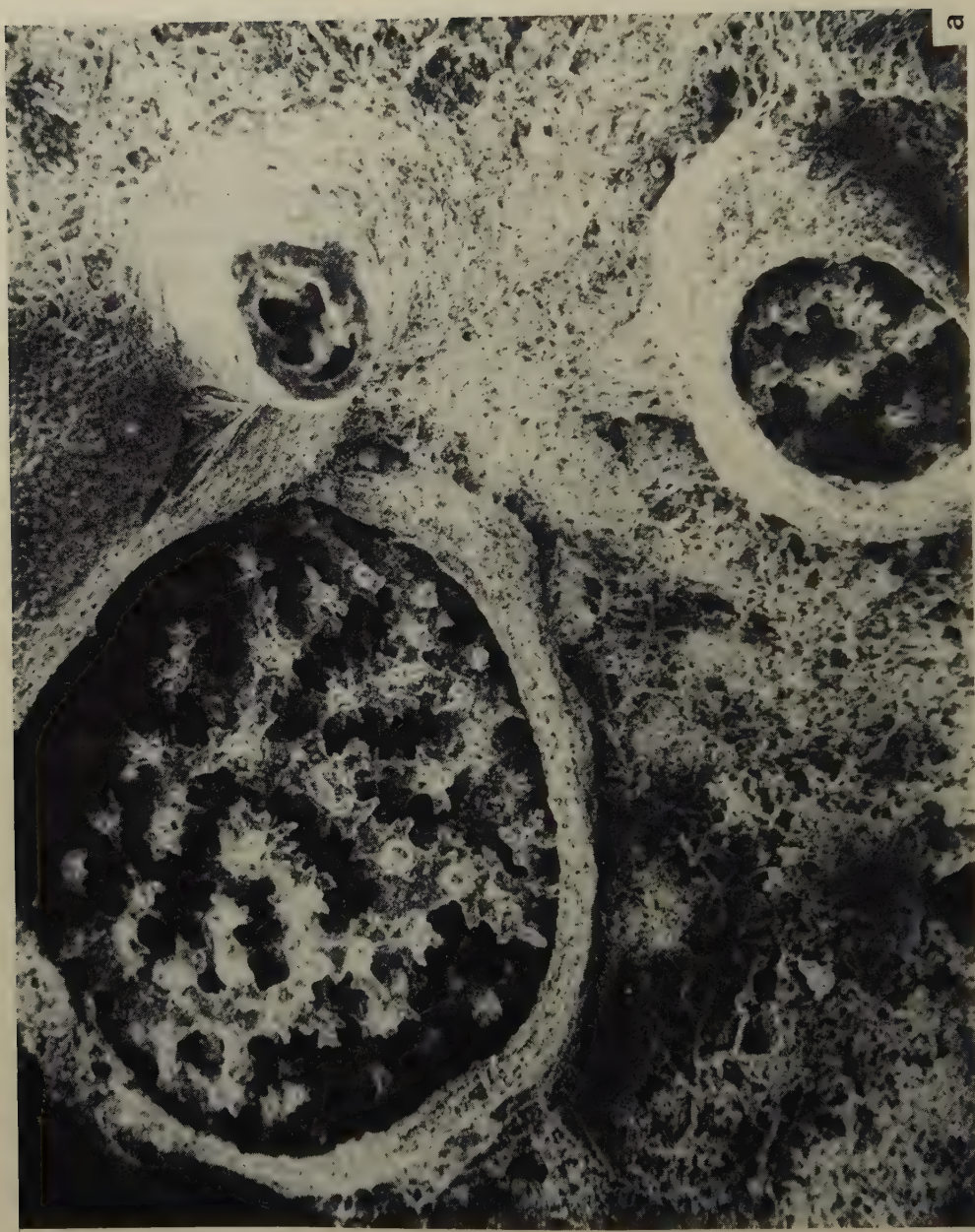

Fig. 17a. For legend see p. 267.

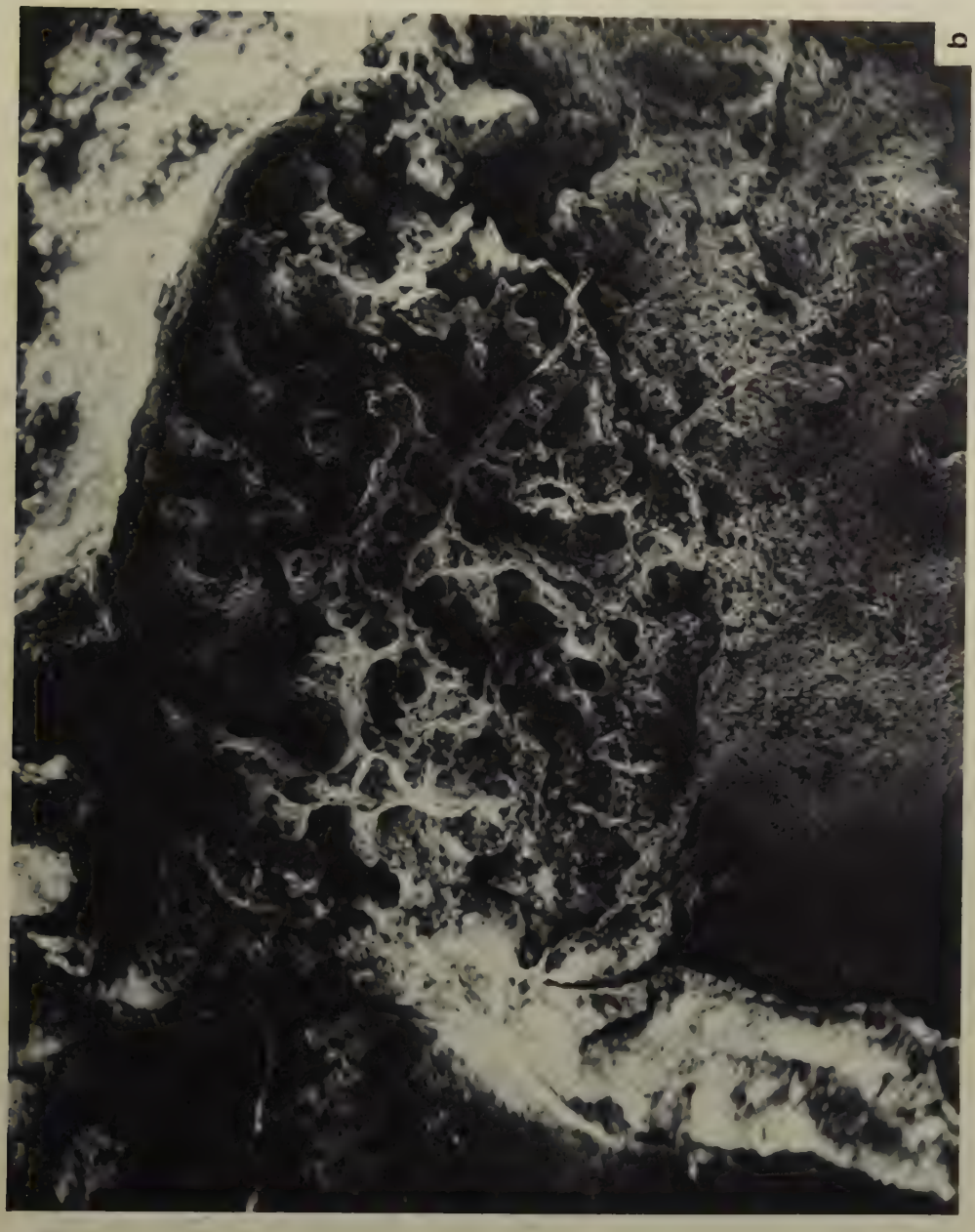

Fig. 17b. For legend see p. 267.

of grazing. The bimodal response observed is probably not typical but merely exemplary of the type of variation possible with older, more highly eroded natural substratum. These results generally agree with Brock's (1979) study on grazing by parrotfish.

Those few corals which survived intense grazing were found predominantly in cryptic microhabitats. Newman (1960) proposed and Stephenson (1961) and Stephenson & Searles (1960) demonstrated that exposure to fish grazing in tropical seas is a major source of mortality for intertidal organisms. I believe these findings may be extended to urchins in the Caribbean subtidal zone. If settlement behaviour in sessile marine invertebrates with mero-planktonic larvae is at least partially genetically determined, then the coral spat in this experiment may have been experiencing selection for cryptic settlement in response to urchin grazing (Lewis, 1974a).

The optimal "state of well-being" and success in competition observed at intermediate *Diadema* densities was probably the result of two opposing forces – competition and biological disturbance. To explain further: (1) In the absence of grazing, competition for space was intense; therefore, due to the high diversity and abundance of associates, relative competitive success in coral spat was low. (2) At high grazing pressures, only the most hardy prey survived – organisms well-adapted to this severe biotic environment. The corals may have been at a disadvantage for two reasons: (a) the cryptic microhabitats probably possessed lower environmental light levels than exposed ones, and light is necessary for normal growth in juvenile hermatypic corals (Lewis, 1974b); (b) biological disturbance and browsing may have damaged and weakened some colonies. A decrease in the intensity of both these factors plus changes in the numbers and composition of competitors probably provided an optimal balance for corals at intermediate *Diadema* densities. It is also possible that increased sedimentation magnifies these processes.

This pattern of optimization was further supported by observations on coral growth. In *Agaricia* and *Porites*, realized colony size was higher at moderate *Diadema* densities where coral recruitment was still relatively high. This was probably the result of relatively high competitive success combined with low disturbance levels. *Favia*, on the other hand, seemed better adapted for coexistence with algae at very low grazing intensities. Different coral species appear to grow best under different sets of biotic circumstances imposed by *Diadema antillarum*.

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BEHAVIORAL AND RHYTHMIC ASPECTS OF FILTRATION IN THE BAY SCALLOP, *ARGOPECTEN IRRADIANS CONCENTRICUS* (Say), AND THE OYSTER, *CRASSOSTREA VIRGINICA* (Gmelin)[1]

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Abstract: Hourly measurements, for periods of 24 to 33 h, were made in the laboratory of filtration rate and cell clearance rate of 39 individual *Argopecten irradians concentricus* (Say) and *Crassostrea virginica* (Gmelin). Bivalves fed on suspensions of algae (*Dunaliella tertiolecta* Butcher, *Isochrysis galbana* Parke, or *Thalassiosira pseudonana* (Hustedt)) whose concentration was maintained at a nearly constant level throughout each experiment. Neither local tidal sequence nor laboratory day : night cycles exerted a significant influence on scallop or oyster filtration behavior. In *Argopecten irradians* filtration activity either remained relatively constant throughout the experimental period or stabilized at a constant level after an initial period of steady decline. There was an inverse relationship between suspended algal concentration (0.94–9.66 mg · l^{-1}) and filtration rate of *A. irradians*, so that the average amount of algae cleared hourly was similar throughout this range of concentrations. Mean filtration rate for all experiments with scallops was 4.7 l · h^{-1} · g dry wt^{-1}, but averaged 5.7 l · h^{-1} · g dry wt^{-1} when ambient concentration was <1.5 mg · l^{-1}. Filtration behavior of *Crassostrea virginica* was generally characterized by alternating periods of high and low activity. Peaks of oyster filtration activity occurred two to three times per day, and the period between peaks did not vary with experimental algal concentration (1.7–6.7 mg · l^{-1}). Oysters filtered actively for 80% of all hourly periods in suspensions of *Thalassiosira pseudonana* and 91% in suspensions of *Isochrysis galbana*; mean filtration rate for *Crassostrea virginica* was 1.5 l · h^{-1} · g dry wt^{-1} for all measurements, and 1.9 l · h^{-1} · g dry wt^{-1} during hourly periods of active filtration. These results indicate that scallops can collect food continuously, and, in the range of concentrations of suspended matter typical of coastal environments, can respond to environmental variations quickly enough to collect a relatively constant supply of food over time. In similar concentrations, filtration of oysters is much more variable. Fluctuations in filtration of oysters in the laboratory could not be related to tidal or diurnal cycles or to food availability. Although their frequency does suggest a tidal component in filtration, the most probable explanation for variations in cell clearance rate is that they serve to regulate food levels in the stomach to permit a relatively constant level of intracellular digestion.

INTRODUCTION

Although a considerable amount of interest has centered on determining pumping and filtration rates of bivalves (see review by Jorgensen, 1975; Winter, 1978), most studies have emphasized either maximal filtration rates attainable under ideal laboratory conditions or average filtration rates of populations over short (1- to 2-h) periods of time.

Yet it is well known that temporal variations in pumping rate, filtration rate, and

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filtration efficiency are components of normal feeding behavior in bivalves. Such variations may be mediated by any of a number of exogenous factors (concentration of suspended particles, diurnal cycles, tides), by endogenous rhythms, or by other factors which seem to bear no temporal relationship to obvious environmental cycles. Because of the difficulty of obtaining reliable long-term (over 24-h) records of filtration behavior and because of the wide variety of experimental techniques used in studies of bivalve feeding, there is little agreement on the importance of these exogenous and endogenous factors in the behavior of individual organisms.

In this study hourly measurements of cell clearance and filtration rate of bay scallops, *Argopecten irradians concentricus* (Say), and oysters, *Crassostrea virginica* (Gmelin), were made under controlled laboratory conditions. Three species of algae were used as food in concentrations of suspended organic matter representative of estuarine and nearshore environments. All experiments were performed on individual bivalves to highlight potential endogenous rhythms of activity. Previous studies have recorded shell movement of individual bivalves over long periods (Loosanoff & Nomejko, 1946; Loosanoff & Engle, 1947; Higgins, 1980), but this is the first study to report variations in cell clearance and filtration behavior of individual bivalves for periods exceeding 24 h.

Materials and Methods

Experimental animals: collection and acclimation

Argopecten irradians concentricus, reared in a hatchery and subsequently released into enclosures in a shallow bay near Virginia Institute of Marine Science, Wachapreague, Virginia, were collected in June 1978, October 1978, and May 1979. The age of all scallops was 6 to 8 months at time of collection. Initial mean shell heights for the three groups were 37.0, 41.6, and 47.1 mm; mean wet weights were 10.7, 15.0, and 20.5 g. *Crassostrea virginica* were removed from rocks 30–50 cm below mean low water near the College of Marine Studies Harbor, Lewes, Delaware in November 1978, and April 1979. Initial mean shell heights for the two groups of oysters were 66.9 and 86.3 mm; mean wet weights were 31.1 and 52.9 g. All experimental animals in this study had a history of continuous submergence, albeit often in very shallow water.

All bivalves were acclimated in an 80-l holding tank with recirculating sea water for at least 10 days prior to experimentation. Temperature in the holding tank was 21 ± 1 °C; when ambient water temperature at time of collection was <21 °C, temperature in the holding tank was raised at the rate of 0.5 °C/day. Organisms were held in sea water (S, 32‰) collected at Indian River Inlet, Delaware at high tide, filtered through cartridge filters to remove particles >0.5 μm, and passed through an activated charcoal filter. Water in the acclimation tank was changed about twice a week, although feces and pseudofeces were siphoned from the tank daily.

During acclimation periods, animals were provided with a constantly dripping supply of algal culture – the same species used later experimentally. Daily ration varied according to species of bivalve and alga used: June 1978 and October 1978 scallops were fed about 2×10^8 cells · g whole animal weight $^{-1}$ · day^{-1} of the diatom *Thalassiosira pseudonana* (Hustedt) Haisle and Heimdal; November 1978 oysters were fed 1.0×10^8 cells · g^{-1} · day^{-1} of the same alga; April 1979 oysters received about 1.5×10^7 cells · g^{-1} · day^{-1} each of the flagellates, *Dunaliella tertiolecta* Butcher and *Isochrysis galbana* Parke; May 1979 scallops received about 3×10^7 cells · g^{-1} · day^{-1} of each of these algal species. The continuous feeding schedule ensured that during the acclimation period, animals were constantly exposed to relatively low concentrations of particulate matter – generally < 3 mg · l^{-1}. Under these conditions growth of bivalves in the acclimation tank was rapid, often approaching that shown in the field immediately prior to collection.

June 1978 scallops were held in the laboratory under constant illumination of ≈ 10 μW · cm^{-2}. All other experimental organisms were maintained under conditions of 12 h light (5 μW · cm^{-2}) : 12 h dark.

ALGAE

Algae were cultured in 40-l carboys at 18 ± 1 °C under continuous cool white fluorescent illumination of ≈ 800 μW · cm^{-2}. *Thalassiosira pseudonana* were cultured in Guillard and Ryther's (1962) F-medium; *Dunaliella tertiolecta* and *Isochrysis galbana* were cultured in F-medium without silicate. Sea water (S, 32‰) for algal culture was collected from Indian River Inlet at high tide, filtered through cartridge filters to remove particles > 0.5 μm, passed through an activated charcoal filter, and pasteurized. Carboys were bubbled gently with an air: CO_2 (2%) mixture.

EXPERIMENTAL PROCEDURES

Thirty-nine feeding studies were conducted during 1978–1979 on individual specimens of *Argopecten irradians* and *Crassostrea virginica* for periods ranging from 24 to 33 h. Algal cells removed from the experimental aquarium by the filtering activity of the organism were replaced every hour so that algal density remained relatively constant throughout the experiment (cf. method of Winter, 1969; Epifanio & Ewart, 1977). In this way, 547 and 471 hourly measurements of filtration rate were generated for *Argopecten irradians* and *Crassostrea virginica*, respectively. For statistical tests, data from part or all of six experiments were judged to be unreliable due to growth of small flagellates in the experimental tanks, so that a total of 848 hourly measurements were ultimately analyzed.

Each experiment was conducted in a 19-l aquarium with 12 to 17 l of filtered Indian River sea water (S, 32‰), which was recirculated with a Metaframe filter pump. For Experiments 1 to 8, lighting was dim (10 μW · cm^{-2}): 12 h off (Table I). Four to 5 h prior to initiation of filtration measurements an individual scallop or

oyster was removed from the acclimation tank, placed in the aquarium onto a plastic mesh platform (which minimized recirculation of feces and pseudofeces), and algal suspension was added to the aquarium. During this acclimation period, most of the scallops formed a byssal attachment to the mesh platform. All animals were actively feeding before all experiments so that behavioral artifacts due to starvation (Winter & Langton, 1975; Starkweather, 1978) were eliminated.

TABLE I

Summary of acclimation and experimental conditions for feeding studies of individual specimens of *Argopecten irradians* and *Crassostrea virginica*: 3H, *Thalassiosira pseudonana*; Ig, *Isochrysis galbana*; Dt, *Dunaliella tertiolecta*.

	Acclimation conditions			Experimental conditions		
Expt. no.	Species of bivalve and collection date	Bivalve growth during acclimation period	Lighting conditions	Species of alga	Range of algal cells · ml^{-1} × 1000	Mean* and range of suspended particulate matter (mg · l^{-1})
1–8	*A. irradians* 5 June 1978	Shell ht: 122 μm · day^{-1} Wet wt: 1.20% · day^{-1}	Continuous (10 μW · cm^{-2})	3H	75–250	3.15 (2.00–7.21)
9–12 15–16	*A. irradians* 24Oct. 1978	Shell ht: 144 μm · day^{-1} Wet wt: 1.75% · day^{-1}	12 h on (5 μW · cm^{-2}): 12 h off	3H	50–340	3.12 (1.32–9.66)
13–14 17–22	*C. virginica* 3 Nov. 1978	Wet wt: 0.17% · day^{-1}	12 h on (5 μW · cm^{-2}): 12 h off	3H	50–150	3.00 (1.67–4.38)
23–32	*C. virginica* 27Apr.1979	Wet wt: 0.05% · day^{-1}	12 h on (5 μW · cm^{-2}): 12 h off	Ig (23–30) Dt (31–32)	30–200	3.74 (1.72–6.80)
33–39	*A. irradians* 30May1979	Wet wt: 0.20% · day^{-1}	12 h on (5 μW · cm^{-2}): 12 h off	Dt	10–30	1.53 (0.94–3.09)

* Particulate organic content was calculated by assuming that algae were neutrally buoyant in sea water and multiplying packed volume of algal cells per liter (value obtained from Coulter Counter) by 1.022 (density of sea water at 20 °C and 32‰ *S*).

All algae used in these studies were isolated in the dark for at least 12 h prior to use to minimize algal division in the experimental tank. *Thalassiosira pseudonana* and *Isochrysis galbana* were harvested directly from algal culture vessels for use in bivalve feeding studies, but *Dunaliella tertiolecta* was centrifuged and resuspended in filtered sea water before use. In control tanks with no bivalves present changes in algal concentration were found to be negligible for periods of up to 15 h; changes in algal concentration which were observed in control tanks were small ($<5\%$) in

relation to changes which would be expected due to the filtering activity of a scallop or oyster.

Thalassiosira pseudonana was initially selected as a desirable algal species for these studies because of its high food value for oysters and scallops (Epifanio, 1979) and because of its size. Ideally, algae used in filter-feeding studies should be small (Schulte, 1975), but not so small as to be inefficiently removed from suspension by the filter-feeder. In 1978, *T. pseudonana* cultured in our laboratory had a median cell volume of 35 μm^3 and a median cell length of 5 to 6 μm. By spring 1979, however, median cell volume for *T. pseudonana* had dropped to 18 μm^3, which was deemed too small to be efficiently filtered, especially by scallops (Mohlenberg & Riisgard, 1978). Therefore experiments conducted during 1979 utilized either *Isochrysis galbana* or *Dunaliella tertiolecta*. These two algal species had median cell volumes of 35 μm^3 and 110 μm^3, respectively. Assuming that the algae were neutrally buoyant in sea water of specific gravity 1.022, median calculated cell weights were 36 and 112 pg, respectively.

Following the bivalve's acclimation period of 3 to 5 h in the experimental aquarium, algal concentration was adjusted to the desired concentration (see Table I for range of concentrations). Every hour thereafter until termination of the experiment, cell concentration was measured and brought back to the original concentration by addition of stock algal culture. The actual cell concentration varied by 5 to 25%, depending upon initial cell concentration. Algae were counted and measured with a Coulter Counter Model Z_B fitted with a 70-μm aperture. Each hour, two replicate samples were taken from each aquarium, and either two or five counts taken on each replicate sample, depending on whether 500 μl or 50 μl of sea water, respectively, were processed. None of the sea water in the aquarium was replaced during the course of the experiment.

At the end of each experiment the bivalve's meats were cleaned from the shell and placed in an oven for 96 h at 65 °C for dry weight determinations.

CALCULATIONS AND STATISTICAL METHODS

Hourly weight-specific filtration rates (FR) were calculated using the equation (Coughlin, 1969):

$$FR = \frac{V}{W} \ln (conc_i/conc_f),$$

where V = volume of experimental aquarium, W = dry weight in grams, and $conc_i$ and $conc_f$ are cell concentration at the beginning and end of each hour. In addition, an hourly weight-normalized filtration rate (FR_n) was calculated:

$$FR_n = FR_0(W_0^{0.34}),$$

where FR_n = filtration rate normalized to a 1-g (dry weight) animal, FR_0 = observed filtration rate, and W_0 = dry weight in grams. FR_n may be defined as the filtration

rate which an animal of weight W_0 would have if its dry weight were 1.00 g and if the population of which that specimen was a member showed filtration behavior which conformed to the relationship $FR = aW^b$. Weight-specific values of b for bivalves of similar size to those used in this study generally range from -0.2 to -0.4 (Winter, 1978). The value of -0.34 used here was first suggested by Epifanio *et al.* (1975) for *Crassostrea virginica*. Kirby-Smith (1972) gave a value of -0.416 for *Argopecten irradians*.

Calculation of weight-normalized filtration rates allows the effect of animal size to be eliminated as a contributor to variations in filtration rate. Thus, one may consider the effect of tidal or daylight variations on filtration rate without accounting for the effects of variations in size of organisms used in the experiments. Use of this normalization technique is most appropriate when experimental animals are of similar size since the exponent b in the allometric equation may change with different size classes (Winter, 1973, 1978; Bayne *et al.*, 1976). Range of size of animals used in these studies was relatively narrow (Table II). Crowley (1973) used a mathematically identical size-normalization technique in a study of filtration of *Daphnia pulex*, although in that case all rates were normalized to a 2-mm animal.

TABLE II

Range of sizes of experimental animals used in filtration studies.

Species	Shell height (mm)	Whole wet wt (g)	Dry tissue wt (g)
Argopecten irradians	39.8–49.3	15.1–23.3	0.512–1.290
Crassostrea virginica	60.5–98.8	29.7–77.2	0.600–1.891*

* Fifteen of 18 oysters had dry wt between 1.00 ± 0.25 g.

For consideration of effect of tidal stage, if any, upon filtration rate of animals kept in the laboratory for at least 10 days, local (Lewes) tidal stage at the time of each hourly measurement of filtration activity was expressed by means of a simple code: each measurement was considered to have been taken at either high tide, low tide, or at one of these states + 1 to 6 h. Tidal stage at time of collection of scallops in Wachapreague was deemed to be irrelevant since differences in tidal sequences between Lewes and Wachapreague are < 1 h. For ANOVA analyses effect of time of day on filtration rate for each bivalve species was investigated by partitioning filtration measurements into 24 hourly groups, effect of tidal stage was studied by partitioning filtration measurements into 14 tidal groupings, and effect of light was studied by partitioning filtration measurements into two groupings (lights on or off). Regression analyses for each bivalve species compared the average cell concentration during each hour of filtration to the filtration rate, the number of cells cleared, or the number of cubic micrometers of algae cleared during that hour.

For investigation of possible endogenous or exogenous rhythms of filtration in experimental animals, 3-h running means of weight-normalized filtration rates were transformed with Fast Fourier analysis (Otnes & Enochson, 1972). The time-series analysis computer package used in this study is described by Martin (1977). The relative amplitudes of the major periods (spectral density) were then calculated and plotted for each experimental organism.

Results

BIVALVE GROWTH DURING ACCLIMATION PERIOD

Experimental animals were weighed and measured regularly during the acclimation period to insure that they had adapted to laboratory conditions and were growing prior to experimentation. Table I gives the results of these measurements. All groups of bivalves showed positive changes in whole animal weight during the acclimation period. Scallops cultured on *Thalassiosira pseudonana* showed the greatest growth (1.20–1.75% per day). Oysters showed slow, steady growth (0.05–0.17% per day). Scallops cultured on *T. pseudonana* added ≈ 1 mm shell height per week, which is about two-thirds the rate of growth reported by Kirby-Smith & Barber (1974) for *Argopecten irradians* kept in flowing sea water with high algal content at 22 °C.

FILTRATION BEHAVIOR

Scallops and oysters showed different patterns of filtration behavior. Of 15 scallop experiments which extended for more than 26 h, eight animals had relatively constant rates of filtration for the entire experimental period (i.e., Experiment 5, Fig. 1a). In another five experiments, filtration rate declined steadily for 10 to 15 h, then stabilized at a relatively constant level for the duration of the experiment (i.e., Experiment 2, Fig. 1b). In only two cases was there evidence of alternating periods characterized by high and low rates of cell clearance and filtration, and one of these two cases was the only experiment in which a scallop fed on uncentrifuged *Dunaliella tertiolecta*. Hour-to-hour variations in filtration in scallops tended to be minor, and in no cases did scallops cease clearing cells from suspension.

In oysters, on the other hand, alternating periods of high and low cell clearance and filtration rate were the rule rather than the exception. In 10 of 15 experiments analyzed, including all of the experiments in which oysters were fed *Thalassiosira pseudonana*, filtration behavior was best described as fluctuating over 3- to 12-h periods between extremes of activity. In Experiment 20, for example, 3-h running mean of weight-normalized filtration rate varied from 0 to 4.42 $l \cdot h^{-1} \cdot g^{-1}$ (Fig. 1c). In other cases, filtration activity never ceased but continued to show large variations; in Experiment 21, for instance, filtration rate ranged from 0.10 to 1.86 $l \cdot h^{-1} \cdot g^{-1}$

(Fig. 1d). In only three cases was oyster filtration activity relatively constant over the course of the experiment, and even in these cases, variations in activity were much larger than with scallops (i.e., Experiment 25, Fig. 1e). In the other two oyster experiments, both with animals fed *Dunaliella tertiolecta*, filtration activity was best described as sporadic in that animals only cleared particles during about one-half of the hourly periods of measurement (Table III).

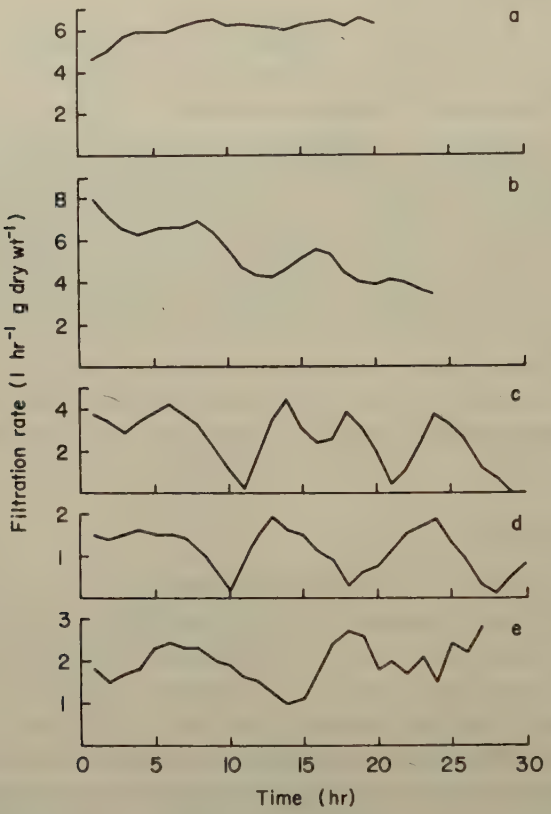

Fig. 1. Representative long-term patterns of filtration activity for individual specimens of *Argopecten irradians* and *Crassostrea virginica*: the ordinate plots 3-h running means of weight-normalized filtration rate; a and b, *A. irradians*; c, d and e, *C. virginica*; for explanation see text.

The relatively constant filtration activity of *Argopecten irradians*, as opposed to the fluctuating activity of *Crassostrea virginica*, was suggested quantitatively by data on means and standard deviations of hourly filtration rate measurements (3-h running means) for 30 individual experiments (Table IV). For the 15 longest running scallop experiments, average value for standard deviation (1.190) was 24.0% of the mean (4.854). Filtration rate for an individual oyster experiment was much more variable, standard deviation (0.794) averaging 59.2% of the mean value (1.522).

Standard deviation exceeded 40% of the mean value in only 2 of 15 scallop experiments, but in 11 of 15 oyster experiments. The apparent qualitative difference in filtration behavior between the two species of bivalves was also suggested quantitatively by the results from Fast Fourier analysis. The length of the data sets limited calculation of power spectra to frequencies of 2/32, 3/32, 4/32, 5/32, ... $16/32 \cdot h^{-1}$,

TABLE III

Crassostrea virginica and *Argopecten irradians*: weight-normalized (to a 1 g dry wt animal) average hourly filtration rates (FR) ($l \cdot h^{-1} \cdot g^{-1}$).

Bivalve species	Algal species	Lighting	Number of FR measurements	Mean (SD) of FR	Range of FR	% of h where FR = 0	Mean FR during h of active filtration
C. virginica	*Thalassiosira pseudonana*	Day and night	185	1.901 (1.721)	0–5.47	20.0	2.376
	Isochrysis galbana	Day and night	172	1.413 (1.156)	0–4.57	9.3	1.557
	Dunaliella tertiolecta	Day and night	55	0.621 (0.828)	0–3.04	50.9	1.264
	All	Day	230	1.482 (1.516)			
	All	Night	182	1.582 (1.370)			
		Total	412	1.526 (1.452)		19.7	1.900
A. irradians	*Thalassiosira pseudonana*	Day and night	259	4.022 (1.646)	0.31–8.78	0.0	
	Dunaliella tertiolecta	Day and night	177	5.684 (2.600)	0.65–11.90	0.0	
	All	Day	218	4.710 (2.151)		0.0	
	All	Night	218	4.683 (2.327)		0.0	
		Total	436	4.697 (2.258)		0.0	

or periods of 16.0, 10.7, 8.0, 6.4, ... 2.0 h. Use of Fourier analysis on a theoretical data set consisting of 32 h of continuous and nearly equal filtration activity would result in a spectrum characterized by maximum power at a period of 16 h and steadily tapering power values down to a period of 2 h (Wayne Martin, pers. comm.). Of 16 scallop experiments examined with Fourier analysis, 15 showed maximal spectral density at a period of 16 h. On the other hand, 9 of 14 oyster experiments showed secondary peaks of spectral density, that is, maximum spectral density occurred at a period of 8.0 to 10.7 h. For example, in Experiment 20 (Fig. 1c) maximal spectral density occurred at a period of 8 h, and in Experiment 21 (Fig. 1d) twin peaks occurred at periods of 10.7 and 8.0 h. These results indicate that much more of the temporal variation in filtration rate for oysters can be explained by endogenous sinusoidal variations with periods of 8.0 to 10.7 h than is the case for scallops.

Table III summarizes weight-normalized filtration rate values for scallops and oysters feeding on three different algal species and during periods of light and darkness. For all lighting conditions and with all feeding suspensions filtration activity was considerably higher for scallops (overall mean value: 4.70 $l \cdot h^{-1} \cdot g^{-1}$) than for oysters (1.53 $l \cdot h^{-1} \cdot g^{-1}$).

TABLE IV

Mean ($\bar{X}$) filtration rate ($l\ h^{-1} \cdot g$ dry wt^{-1}) and SD for each of 30 experiments: the 15 longest-running experiments with each species (*Argopecten irradians* and *Crassostrea virginica*) were selected for analysis; each mean value is based on an average of 26 consecutive hourly measurements.

Argopecten irradians				*Crassostrea virginica*			
Expt. no.	$\bar{X}$	SD	SD as % of $\bar{X}$	Expt.	$\bar{X}$	SD	SD as % of $\bar{X}$
1	2.842	0.903	31.8	17	2.724	0.969	35.6
2	5.311	1.299	24.5	18	1.832	1.266	69.1
5	6.114	0.284	4.6	19	2.504	1.973	78.8
6	4.723	0.578	12.2	20	2.451	1.319	53.8
7	3.471	0.793	22.8	21	1.111	0.504	45.4
8	4.199	0.542	12.9	22	0.761	0.539	70.8
9	4.825	0.491	10.2	23	1.961	0.350	17.8
10	3.736	0.210	5.6	24	3.350	0.749	22.4
33	3.250	2.224	68.4	25	1.136	0.916	80.6
34	5.684	0.663	11.7	27	1.022	0.837	81.9
35	5.462	1.753	32.1	28	0.820	0.297	36.2
36	6.786	3.064	45.2	29	0.835	0.332	59.2
37	5.502	1.466	26.6	30	1.071	0.763	71.2
38	6.615	0.085	12.2	31	0.377	0.393	104.2
39	7.129	2.772	38.9	32	0.876	0.705	80.5
Mean	4.854	1.190	24.0	Mean	1.522	0.794	59.2

For *C. virginica*, filtration rate was highest in suspensions of *Thalassiosira pseudonana* (1.90 $l \cdot h^{-1} \cdot g^{-1}$), intermediate with *Isochrysis galbana* (1.41 $l \cdot h^{-1} \cdot g^{-1}$), and lowest with *Dunaliella tertiolecta* (0.62 $l \cdot h^{-1} \cdot g^{-1}$). Mean filtration rates were significantly different for all three species of algae ($P < 0.01$). Oysters actively pumped during 91% of the hourly periods in suspensions of *Isochrysis galbana*, 80% of the time with *Thalassiosira pseudonana*, and only 49% with *Dunaliella tertiolecta*. There was little difference in filtration activity between periods of light and darkness. Filtration rate exceeded 3.00 $l \cdot h^{-1} \cdot g^{-1}$ for 17% of all hourly periods, and exceeded 4.00 $l \cdot h^{-1} \cdot g^{-1}$ for only 5% of all periods.

For *Argopecten irradians*, filtration rate was significantly higher in suspensions of *Dunaliella tertiolecta* (5.68 $l \cdot h^{-1} \cdot g^{-1}$) than in suspensions of *Thalassiosira pseudonana* (4.02 $l \cdot h^{-1} \cdot g^{-1}$) ($P < 0.01$). Mean particulate levels were about twice as high in experiments with *T. pseudonana* (3.14 $mg \cdot l^{-1}$) as with *Dunaliella tertiolecta*

(1.53 mg · l $^{-1}$). Scallops actively pumped during every one of the 436 h of filtration measurements, and there was virtually no difference in filtration rates between periods of light and darkness. Filtration rate exceeded 10 l · h $^{-1}$ · g $^{-1}$ during 8% of all periods when *D. tertiolecta* was used as food and exceeded 6 l · h $^{-1}$ · g $^{-1}$ during 18% of all periods when *Thalassiosira pseudonana* was used as food. Filtration rate or *Argopecten irradians* fell below 1.00 l · h $^{-1}$ · g $^{-1}$ in only 6 of 436 periods, and four of these occurred when suspended particulate matter (*Thalassiosira pseudonana*) was highest (>9.0 mg · l $^{-1}$). During only 5% of all experimental periods did filtration for scallops drop below 2 l · h $^{-1}$ · g $^{-1}$, and during all 22 of these periods particulate content exceeded 5 mg · l $^{-1}$.

STATISTICAL RESULTS

Table V summarizes results from statistical tests of the effects of tidal stage, time of day, lighting conditions, and average cell concentration on filtration rates of

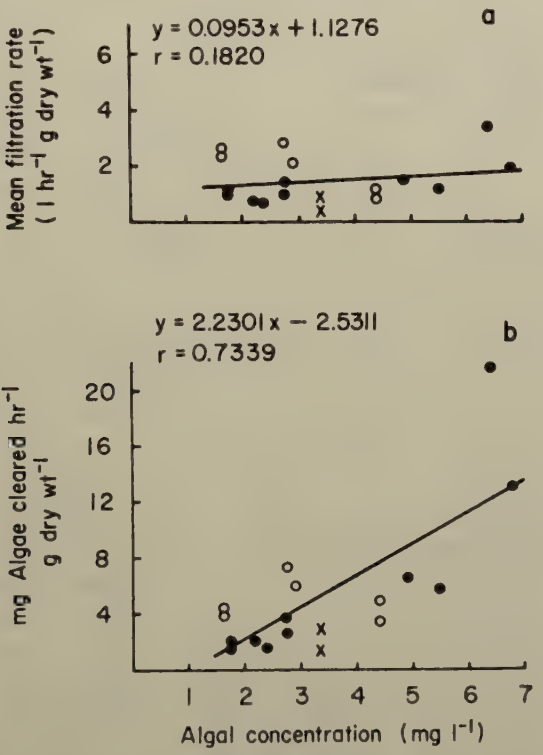

Fig. 2. Relationship between suspended algal concentration (mg · l $^{-1}$) and both mean hourly filtration rate (a) and mean hourly amount of algal clearance (b) for *Crassostrea virginica*: each point represents the mean value for the experiment – that is, for 10 to 33 hourly measurements of filtration rate or cell clearance; algae used were *Dunaliella tertiolecta* (×), *Isochrysis galbana* (●), or *Thalassiosira pseudonana* (○).

TABLE V

Crassostrea virginica and *Argopecten irradians*: results from statistical tests for effects of tide, time of day, lighting, and average cell concentration on weight-normalized filtration rates of individual bivalves in laboratory experiments: ns, not significant at 0.05 level; * $P < 0.05$; ** $P < 0.01$; 3H, *Thalassiosira pseudonana*; Ig, *Isochrysis galbana*; Dt, *Dunaliella tertiolecta*; hourly data were used for ANOVAs and *t*-tests; average filtration rates for individual experiments were used for regression analyses; *a*, y-intercept; *b*, slope of regression equation; *r*, correlation coefficient.

Statistical analysis	All scallops	Scallops fed 3H	Scallops fed Dt	Scallops exposed to 12 : 12 light	All oysters	Oysters fed 3H	Oysters fed Ig
Tide vs. filtration (one-way ANOVA)	ns	ns	ns		ns	ns	ns
Time of day vs. filtration (one-way ANOVA)	ns	*	**	ns	ns	ns	ns
Day : night vs. filtration (*t*-test)	ns	** Day = 4.33 Night = 3.74	* Day = 5.23 Night = 6.19	ns	ns	ns	ns
Average concentration ($mg \cdot l^{-1}$) vs. algae cleared ($mg \cdot h^{-1}$) (regression)	$a = 8.135$ $b = 0.513$ $r = 0.345$	$a = 10.038$ $b = 0.209$ $r = 0.136$			$a = -2.531$ $b = 2.230$ $r = 0.734$	$a = 5.067$ $b = -0.078$ $r = 0.064$	$a = -4.358$ $b = 2.750$ $r = 0.841$
Average concentration ($mg \cdot l^{-1}$) vs. filtration regression	$a = 6.364$ $b = -0.649$ $r = 0.896$	$a = 5.997$ $b = -0.586$ $r = 0.888$			$a = 1.128$ $b = 0.095$ $r = 0.182$	$a = 3.758$ $b = -0.610$ $r = 0.897$	$a = 0.229$ $b = 0.295$ $r = 0.731$

Argopecten irradians and *Crassostrea virginica*. Neither tidal stage nor time of day had a significant effect on filtration of any of the groups of scallops or oysters. Similarly, filtration activity during daylight did not differ significantly from filtration at night for any of the groups, with two exceptions. *Argopecten irradians* feeding on *Thalassiosira pseudonana* showed a significantly higher mean rate of filtration during daylight hours ($P < 0.01$), and *Argopecten irradians* feeding on *Dunaliella tertiolecta* showed a significantly higher mean rate of filtration during nighttime hours ($P < 0.05$). These two effects balanced out, however, so that for all scallops differences in filtration during day and night were not only statistically insignificant (Table V) but also inconsequential (4.71 $l \cdot h^{-1} \cdot g^{-1}$ and 4.68 $l \cdot h^{-1} \cdot g^{-1}$, respectively).

The mean filtration rate ($l \cdot h^{-1} \cdot g^{-1}$) and mean weight of algae cleared ($mg \cdot h^{-1}$) during each experiment were plotted as a function of suspended particulate concentration ($mg \cdot l^{-1}$). Results (Table V, Fig. 2) indicated that over the range of concentrations tested filtration behavior as a function of suspended algal concentration differed for the two bivalve species. In *Crassostrea virginica* there was no ap-

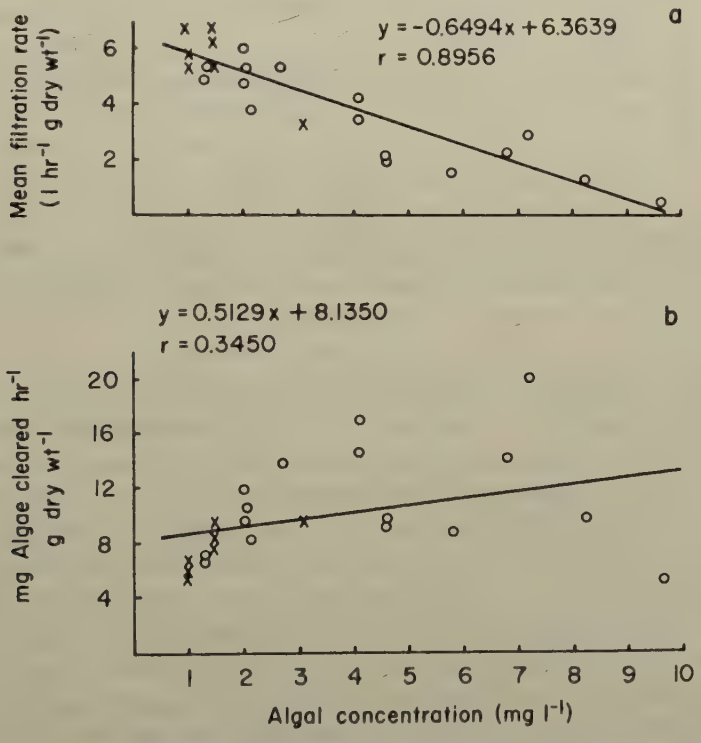

Fig. 3. Relationship between suspended algal concentration ($mg \cdot l^{-1}$) and both mean hourly filtration rate (a) and mean hourly amount of algal clearance (b) for *Argopecten irradians*: each point represents the mean value for one experiment – that is for 5 to 32 hourly measurements of filtration rate or cell clearance; algae used were *Dunaliella tertiolecta* (×) or *Thalassiosira pseudonana* (○).

parent relationship between algal concentration (1.67–6.80 mg · l^{-1}) and filtration rate (Fig. 2a); as a result, over this range of concentration the amount of algae cleared from suspension tended to increase with suspended algal concentrations, although there was a great deal of variability between experiments (Fig. 2b). It is interesting that in experiments in which oysters were fed *Thalassiosira pseudonana* mean filtration rate did decrease with an increase in suspended matter so that average amount of algae cleared was relatively constant over a range of particulate levels from 1.67–4.38 mg · l^{-1} (Fig. 2b). However, such regulation was not evident in experiments in which *Crassostrea virginica* were fed *Isochrysis galbana*.

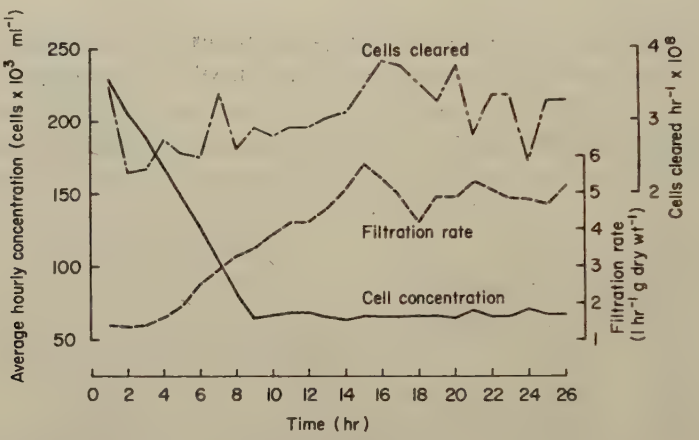

Fig. 4. Regulation of cell clearance by short-term adjustments of filtration rate in *Argopecten irradians*: as suspended algal concentration dropped, hourly filtration rate increased to maintain the amount of algal clearance at a relatively constant level: after Hour 8, suspended algal concentration and filtration rate stabilized.

With *Argopecten irradians* there was a clear-cut inverse relationship between suspended algal concentration (0.94–9.66 mg · l^{-1}) and mean filtration rate (Fig. 3a). As a result, the mean amount of algae cleared from suspension was relatively constant over a wide range of suspended algal concentration (Fig. 3b). A striking example of the inverse relationship between cell concentration and filtration rate of scallops is shown in Fig. 4. In this experiment, an individual scallop reduced the concentration of *Thalassiosira pseudonana* from 242 000 · ml^{-1} to 80 000 · ml^{-1} (7.42–2.45 mg · l^{-1}) over a period of 8 h, after which concentration was adjusted to 80 000 · ml^{-1} by hourly additions of algae. As cell concentration dropped from 242 000 · ml^{-1} to 80 000 · ml^{-1}, filtration rate steadily increased, so that the number of cells removed from suspension stayed virtually constant throughout the 26-h experiment.

Discussion

FEEDING BY *ARGOPECTEN IRRADIANS*

Under the experimental conditions and range of cell concentrations used in these studies, *A. irradians* is best characterized as a continuous feeder whose filtration rate varies with cell concentration in such a way that relatively equal volumes of particles are removed from suspension for periods exceeding 24 h. It is known that the valves of subtidal oysters remain open nearly continuously (Loosanoff & Nomejko, 1946) and that the functional morphology of the pallial and digestive organs of bivalves seems to allow continuous collection and processing of food particles (Owen, 1966, 1974; Purchon, 1968). However, experimental evidence that individual unstarved organisms do, in fact, filter food particles at a steady rate over long periods of time, as has been shown for ascidians (Fiala-Medioni, 1973, 1974, 1978) has not been reported for the bivalves. In most of the present experiments, bay scallops did maintain high rates of filtration and cell clearance for periods of about 30 h. It should be noted, however, that these constant rates of cell removal do not guarantee that scallops ingested and digested food at a constant rate since rate of pseudofecal production might have varied temporally. Such a possibility could be verified only by quantifying both filtration rate and pseudofecal production, without disturbing the experimental organism, at short intervals over long periods of time.

These observations on scallop filtration behavior agree with values recorded in other filtration studies of shorter duration with *A. irradians* and other species of scallops. Data and formulae given by Chipman & Hopkins (1954) and by Kirby-Smith (1972) indicated that filtration rate in *A. irradians* (21 to 25 °C) is ≈ 6.0 $l \cdot h^{-1} \cdot g$ dry wt^{-1}. Average rate in the present experiments was $4.7\ l \cdot h^{-1} \cdot g^{-1}$, but in experiments utilizing dilute suspensions of *Dunaliella tertiolecta* filtration rate was $5.7\ l \cdot h^{-1} \cdot g^{-1}$. Similarly, McLusky (1973) found that filtration rate of *Chlamys opercularis* varied from 4.0 to $5.7\ l \cdot h^{-1} \cdot g^{-1}$, from 5 to 20 °C, with a maximum rate at 15 °C.

No tidal or diurnal effects on filtration rate of *Argopecten irradians* were observed in this study. Mathers (1976) found that *Pecten maximus* tend to physically orient toward either the running or ebbing tidal flow in Galway Bay, Ireland and concluded that filtration activity for an individual scallop was restricted to part of each tidal cycle; Mathers (1976) speculated, however, that this was a local phenomenon caused by strong reversible tidal flow and probably not an endogenous feature of scallop feeding behavior. Therefore, the lack of tidal patterns in filtration behavior of *Argopecten irradians* in the present study was not surprising, especially since all organisms in this study were acclimated in the laboratory under nontidal conditions for at least 10 days prior to experimentation.

The lack of diurnal components in filtration behavior was more surprising.

Salanki (1966) described diurnal rhythms of shell adduction in *Pecten jacobeus*, and Yamamoto (1977) showed that filtration rate of spat and juveniles of *Patinopecten yewsoensis* was inversely related to light intensity, peaking at about 300. Furthermore, *Argopecten irradians* does possess a well-defined diurnal rhythm of shell deposition. Daily during summer daylight hours, the mantle extends back over the shell margin for several hours to form a calcareous ridge (Wrenn, 1972; Wheeler *et al.*, 1975). This diurnal rhythm was retained by scallops used in these studies (Palmer, 1980a), and I hypothesized that magnitude of filtration activity would be affected by the reorientation of the mantle edge during shell ridge formation. Such was not the case; mean daylight and nighttime rates of filtration did not differ significantly.

Under experimental conditions used in these studies, filtration rate of *A. irradians* decreased steadily in concentrations of suspended algae >2.0 mg $\cdot l^{-1}$ so that the relationship between algal concentration and algal weight cleared hourly appeared to be rectilinear (Fig. 3b). The inflection point (satiation point) of this curve, that point beyond which the amount of food cleared remained relatively constant, occurred at ≈ 2 mg wet algal wt $\cdot l^{-1}$ so that maximum algal clearance at 21 °C was ≈ 15 mg wet algal wt $\cdot h^{-1} \cdot$ g scallop dry wt^{-1}. Two mg wet algal wt $\cdot l^{-1}$ equals $\approx 57\,000$ cells $\cdot$ ml^{-1} of *Thalassiosira pseudonana* or *Isochrysis galbana* or 18 000 cells $\cdot$ ml^{-1} of *Dunaliella tertiolecta*. The effect of these variations in filtration rate is that a constant ration of food is collected by the gills, even when ambient concentrations of suspended particulates are greater than that needed to ensure maximum growth of the organism. Furthermore, for *Argopecten irradians* such regulation of filtration rate may occur in rapidly changing concentrations of particulate matter (Fig. 4).

Whether bivalves in general regulate filtration rate to compensate for variations in suspended particulate matter is still an open question (see contrasting views of Winter (1978) and Jorgensen (1975)). Most of the long-term experiments with unstarved organisms, however, do indicate that such regulation may be common with estuarine and coastal invertebrate filter-feeders. Winter (1970) showed that the inflection point for *Modiolus modiolus* feeding on *Dunaliella* sp. occurred at 1.1 mg algal dry wt $\cdot l^{-1}$. Williams (1978) found that the satiation point for the gastropod *Crepidula fornicata*, feeding on suspensions of *Dunaliella tertiolecta*, *Isochrysis galbana*, or *Thalassiosira pseudonana* occurred at ≈ 5 mg wet algal wt $\cdot l^{-1}$. The number of algal cells ingested by the copepod *Calanus hyperboreus* did not increase at levels of particulate organic carbon >200 μg $\cdot l^{-1}$ (Conover, 1966); for the colonial bryozoan *Zoobotryon verticillatum*, the satiation point occurred at 5100 cells $\cdot$ ml^{-1} of *Dunaliella tertiolecta* and 7900 cells $\cdot$ ml^{-1} of *Isochrysis galbana* (Bullivant, 1968).

Alteration of filtration rate and volumes of food ingested by bivalves may be affected by any one of seven behavioral mechanisms (Winter, 1978). In the present study *Argopecten irradians* was observed to employ two of these mechanisms. First, shell gape tended to decrease with increases in ambient cell concentrations. Second, in concentrations of suspended algae below 2 mg $\cdot l^{-1}$ the free margin of the gill was

often observed to protrude well beyond the posterio-ventral margin of the shell, an orientation which may have resulted in increased flow of water through the mantle cavity. In denser algal concentrations the gill was never observed to extend beyond the shell margin.

The ability of *A. irradians* to regulate food clearance is probably of importance to natural populations since particulate concentrations utilized in these studies fall well within the range of particulate organic carbon (POC) levels characteristic of rich coastal and estuarine environments. Range of algal concentrations in the present study was 0.94 to 9.66 mg wet algal wt $\cdot l^{-1}$, and maximum algal clearance occurred at $\approx$2.0 mg wet algal wt $\cdot l^{-1}$. In ponds on Martha's Vineyard, Massachusetts (Matthiesen & Toner, 1966) and in Beaufort Channel, North Carolina (Kirby-Smith & Barber, 1974) chlorophyll *a* levels often reached 5 $\mu g \cdot l^{-1}$, indicating living algal carbon levels of $\approx 230\ \mu g \cdot l^{-1}$. Assuming that 75% of the organic carbon was detrital (Chervin, 1978), suspended organic loads in these environments probably easily exceeded 2 mg $\cdot l^{-1}$. POC levels in estuarine Canary Creek, Delaware averaged 3 mg $\cdot l^{-1}$ during the summer months (Palmer & Carriker, 1979). In the Hudson River estuary and the apex of New York Bight, Chervin (1978) found that POC ranged from 0.20 to 2.25 mg $\cdot l^{-1}$, with most of the material being detrital. Widdows *et al.* (1979) measured seston levels of 4.0 to 35 mg $\cdot l^{-1}$ and dry wt of food material at 0.7 to 2.0 mg $\cdot l^{-1}$ in the Lynher estuary in England.

Observations made in laboratory experiments utilizing unicellular algal suspensions can only be extended with caution to populations in the field, where suspended material consists of many algal species, detritus, and inorganic particles. Nevertheless, the regulation of filtration activity in relatively low concentrations of particulates described in this study dovetails with observations by Kirby-Smith & Barber (1974) on growth in *A. irradians*. These authors examined shell growth rate of scallops at four temperatures and at a variety of algal concentrations, as estimated by measurements of chlorophyll *a*. At 22 °C growth of scallops did not increase when chlorophyll *a* concentration increased above 1.2 $\mu g \cdot l^{-1}$, a level which is usually easily exceeded in the summer over scallop beds in both North Carolina (Kirby-Smith, 1972) and Massachusetts (Matthiesen & Toner, 1966). Thus growth of bay scallops in the field may often be limited by temperature, other environmental variables, or the assimilative capacity of the organisms themselves rather than by food availability. During these periods of plentiful food supply the present observations indicate that scallops would continue to clear food at a relatively constant rate and would alter filtration rate to adjust to changing concentration of particulate matter in the environment.

FEEDING BY *CRASSOSTREA VIRGINICA*

For the range of algal cell concentrations used in these studies (1.7–6.8 mg $\cdot l^{-1}$), *C. virginica* is best characterized as a discontinuous feeder which shows fluctuating

rates of cell clearance and filtration rate under constant experimental conditions. Epifanio & Ewart (1977) determined cell clearance values for populations, rather than individuals, of *C. virginica* feeding on algal suspensions. Their data, collected at 4-h intervals for 24 h, also indicated that periods of activity and relative quiescence in filtration occur in oysters exposed to unchanging environmental conditions.

These large temporal fluctuations in filtration activity occurred even though hourly measurements of cell clearance indicated that individual oysters were open and actively pumping nearly the entire experimental period. In suspensions of *Isochrysis galbana*, for instance, oysters actively filtered during 91% of 172 1-h periods. Similarly, Loosanoff & Nomejko (1946), in studies conducted in the field, and Higgins (1980), in laboratory experiments utilizing suspensions of *I. galbana*, showed that valves of *Crassostrea virginica* gape for over 90% of the time. However, the valves of an oyster may remain open for long periods of time without the oyster pumping significant amounts of water (Loosanoff & Engle, 1947), a phenomenon which probably accounts for the marked fluctuations in filtration activity observed in the present experiments. The extremely erratic behavior of *C. virginica* observed in two experiments utilizing *Dunaliella tertiolecta* may have been caused by algal metabolites since these were the only experiments with oysters in which *D. tertiolecta* were not centrifuged and resuspended in filtered sea water. The erratic filtration behavior of oysters in suspensions of *D. tertiolecta* is interesting in light of the poor food value of this alga for oysters (Walne, 1970).

Filtration rate values for *Crassostrea virginica* obtained in the long-term experiments reported here agree closely with direct measurements of pumping activity in this species. Jorgensen (1966) gives an average value for pumping rate of 0.5 $l \cdot h^{-1} \cdot g$ wet tissue wt^{-1} which corresponds to $\approx 2.25\ l \cdot h^{-1} \cdot g$ dry tissue wt^{-1}. The latter value is intermediate between mean filtration rates of *C. virginica* determined in this study during hours of active feeding in suspensions of *Thalassiosira pseudonana* and *Isochrysis galbana* (Table III). The amount of algae cleared by oysters depended on cell concentration. Adult oysters feeding on low concentrations of *Thalassiosira pseudonana* or *Isochrysis galbana* cleared $\approx$3–4 mg algae $\cdot h^{-1} \cdot g$ dry wt^{-1} (Fig. 2b). Juvenile *Crassostrea virginica* studied by Higgins (1980) cleared $\approx 10^7$ cells $\cdot h^{-1} \cdot g$ wet wt^{-1} when feeding on similar concentrations of *Isochrysis galbana*, which corresponds to ≈ 10 mg algae $\cdot h^{-1} \cdot g$ dry wt^{-1}. The difference in cell clearance rates recorded in these two studies is largely due to difference in size of oysters (allometric rate relationship).

The effects of the environmental variables of lighting and tide in the present laboratory experiments were minimal. In earlier field studies Loosanoff & Nomejko (1946) found that opening and closing of the shell of subtidal oysters was not correlated with either daylight or tidal sequence. Furthermore, unlike scallops, there was no apparent influence of suspended algal concentration (1.7–6.8 $mg \cdot l^{-1}$) on filtration rate of oysters and likewise, no clear homeostatic mechanism regulating the amount of material cleared from suspension. It may be that control of food in-

gestion in oysters by regulation of filtration rate or filtration efficiency occurs only at higher concentrations of suspended material than were utilized in these studies. Such regulation of oyster filtration rate has been observed by Loosanoff & Engle (1947), and Epifanio & Ewart (1977); regulation of filtration efficiency at high concentrations was reported by Palmer (1980b). At lower concentrations, control of food ingestion may occur temporally, by aperiodic pumping activity, or mechanically, by formation of pseudofeces, as in *Mytilus edulis* (Foster-Smith, 1975). It is interesting that in experiments with *Thalassiosira pseudonana*, filtration rate of oysters did tend to decrease with increases in algal concentration, whereas the opposite was true for experiments utilizing *Isochrysis galbana*. Epifanio & Ewart (1977) observed a similar paradoxical behavioral response for *Crassostrea virginica* feeding on these same two species of algae.

Fluctuating filtration rates and rates of food clearance in oysters were statistically analyzed in an attempt to confirm one of two hypotheses of bivalve feeding behavior – that feeding and digestion in subtidal bivalves are controlled either by rhythms set by exogenous environmental cycles or by food availability. (Fluctuating patterns of food clearance in oysters seemed to preclude the possibility of continuous and constant feeding and digestion.) If periods of feeding and digestion alternate in concert with environmental cycles, as in subtidal *Ostrea edulis* (Morton, 1971) and *Teredo navalis* (Morton & McQuiston, 1974), then laboratory data on filtration rates would show predictable rhythmical variations which would not change significantly with variations in cell concentration. For instance, an organism possessing a diurnal rhythm of feeding would show peaks of activity separated by periods of 24 h, regardless of ambient cell concentration. On the other hand, if rhythms of feeding and digestion were controlled by patterns of food availability (Langton & Gabbott, 1974; Owen, 1974; Wilson & LaTouche, 1978; Robinson & Langton, 1979), then one would expect that the time period between peaks of activity would vary with ambient concentration of suspended food particles. This second hypothesis represents an endogenous mechanism for control of ingestion and posits that an oyster filters food until its assimilative capacity is exceeded, at which point filtration ceases or slows during a period of active digestion. If this hypothesis is true, one would expect that periods between peaks of food clearance would be shorter in denser concentrations of food material since the organism's assimilative limit would be saturated more quickly in such dense suspensions.

Statistical analyses of oyster filtration data did not definitely support either of these hypotheses. The lack of significance in ANOVA analyses of effects of tide and daylight on filtration activity have already been discussed; it is possible that a tidal rhythm exists in *Crassostrea virginica* but was lost during 10 to 14 days of acclimation in the laboratory. Fourier analyses were employed to test the hypothesis that endogenous rhythms of food consumption are important in explaining fluctuating feeding behavior. If these rhythms were important, then peaks of spectral density should have occurred at shorter time periods when the oyster was exposed to high

food concentrations than when it was exposed to more dilute concentrations. Such was not the case. Peaks of spectral density in oyster filtration records tended to be centered at 10.7 h, regardless of ambient food concentration.

The fact that filtration activity of oysters in this study tended to show 2 to 3 maxima and minima per day is intriguing since activity patterns with similar frequencies have been observed by other workers for *C. virginica* and other species of bivalves. Higgins (1980) found that, on the average, an individual *C. virginica* closed its shell for short periods of time between two and three times per day under constant laboratory conditions. Shell growth lines have been hypothesized to be remnants of periods of shell closure and consequent anaerobiosis (Lutz & Rhoads, 1977; Gordon & Carriker, 1978); Palmer & Carriker (1979) found that undisturbed subtidal oysters deposited an average of 2 to 2.5 growth lines per day on the surface of the shell hinge. Similarly, Winter (1969, 1970) observed that populations of both *Arctica islandica* and *Modiolus modiolus* had roughly two maxima and two minima in food consumption per day under constant conditions.

The similarity of the frequencies in activity patterns in all of these studies suggest that circatidal rhythms of activity may occur in *Crassostrea virginica*, even under constant laboratory conditions. However, these studies are clearly only suggestive, not definitive, on this point and confirmation of this hypothesis will come only after more careful study, preferably in long-term experiments (over 100 h) utilizing individual organisms.

Thus, under constant environmental conditions, variations in oyster filtration activity are pronounced, but cannot be related to exogenous or endogenous rhythms. Higgins (1980) also observed temporal variations in feeding activity of juvenile oysters and noted that, whether fed continuously or discontinuously, oysters consumed food at similar rates when food was present. At the present time, the most reasonable model for oyster feeding and digestion under constant environmental conditions is that they are continuous and simultaneous, and that variations in cell clearance rate serve to regulate food levels in the stomach so as to permit a relatively constant level of intracellular digestion (Palmer, 1980b).

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